

The
American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

Arthur L. Schipper, *Editor*

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Goldfinches on the Hastings Natural History Reservation

Jean M. Linsdale

Hastings Natural History Reservation, Carmel Valley, California

Study of the goldfinches was initiated almost at the beginning of work on the Reservation. Of the four species representing the genus *Spinus* the pine siskin and the American goldfinch come infrequently to the area. The green-backed goldfinch and the Lawrence goldfinch occur here abundantly, but not consistently according to numbers or season. The birds, moreover, are small and generally inconspicuous when they perch in foliage. They tend to return to certain sites for nesting and foraging for food and water. No goldfinches have been trapped or killed for study on the Reservation. Effort was made to avoid disturbance to nests or the near-by surroundings. The evidence obtained came from watching with 8x binoculars at a distance from nests or places where birds assemble.

Mrs. Russell P. Hastings established the Frances Simes Hastings Natural History Reservation in 1937. The land was turned over to the University of California for use by the Museum of Vertebrate Zoology. A primary objective was to provide a tract of land where natural conditions might prevail and allow the soil, the plants, and the native animals to exist undisturbed by the sometimes destructive practices that accompany the prevailing treatment of agricultural land. Another objective was to make studies of each kind of animal on the area to learn how it is able to survive and adapt its mode of living to whatever natural conditions might develop as the effects of protection become operative.

Because the primary effort was to understand the vertebrate species that inhabit the Reservation, the first undertaking was to assemble materials and information that would be needed to validate the observations made on each kind of vertebrate. Our collection and records, therefore, dealt with such topics as geology, soils, climate, weather, vegetation, invertebrates, parasites, food, migrations, interrelations, life cycles, and populations.

Information pertaining to the natural history of the vertebrate species has accumulated in large amount for many animals. We have evidence that demonstrates the behavioral response to the environment at the Reservation. Concentration of effort in this manner seems appropriate because of the rare opportunity to make use of land and animals that are completely protected from human disturbance.

Behavior characteristics of goldfinches, such as salt-eating, nest-fouling,

nesting in colonies, strongly social grouping in nonbreeding season, and well developed flight song, as well as the physical bases for them have been treated as having significance in the taxonomy of the birds (see Tordoff, 1954:16).

In an analysis of the distribution of the birds of California, Miller (1951) has shown that both the green-backed and the Lawrence goldfinches in this state zonally occupy the Lower Sonoran, Upper Sonoran, and the Transition. In that work a selection of ecologic formations was the basis for description and classification of the distribution of the breeding birds of the State. The green-backed goldfinch occupies eight of these formations, as follows: sagebrush, chaparral, piñon-juniper woodland, oak woodland, riparian woodland, savanna, grassland, and coastal forest. The Lawrence goldfinch occupies only five formations, as follows: chaparral, oak woodland, grassland, alpine meadow, and montane forest.

Further indication of adaptability in these two species is shown in the following statements bearing on populations of the goldfinches. In the 26 years after 1924 bird banders in the western United States banded 3888 green-backed goldfinches and 165 Lawrence goldfinches. On the 54th Christmas bird count the total number of green-backed goldfinches counted was 4502 and the largest number (1700) was tallied at Sacramento, California. Corresponding figures for the Lawrence goldfinch were 288 and 168 at Tucson, Arizona.

The following persons made records of their observations on goldfinches on the Reservation and in the years indicated.

Dana L. Abell, 1949	Carl B. Koford, 1950
Lowell Adams, 1939	David Lack, 1939
George A. Bartholomew, 1940	Enid A. Larson, 1951-1955
John E. Chattin, 1940	Jean M. Linsdale, 1937-1955
Gene M. Christman, 1951	Joe T. Marshall, Jr., 1948
Walter W. Dalquest, 1942	João Moojen, 1945
John Davis, 1953	Richard W. Neil, 1941
Floyd E. Durham, 1942-1943	Thane A. Riney, 1941, 1946
Robert B. Finley, Jr., 1946	Thomas L. Rodgers, 1939
Henry S. Fitch, 1937	George M. Scheibner, 1941
Gretchen Graves, 1951	Charles G. Sibley, 1938
John A. Gray, Jr., 1939-1940, 1945	Lloyd P. Tevis, Jr., 1939-1940, 1942, 1946
Richard J. Hitsch, 1941	P. Quentin Tomich, 1942, 1947-1952
Henry A. Hjersman, 1939-1940	Howard Twining, 1938
Robert Holdenried, 1938-1940	Eugene R. Volz, 1953
Douglass H. Hubbard, 1939	Henry G. Weston, Jr., 1944-1945
Everett W. Jameson, 1942	Waldemar L. Wiederhoeft, Jr., 1948
Ernest L. Karlstrom, 1952	

Especially long series of records were made by John A. Gray, Jr., Henry A. Hjersman, and David Lack. Miss Beatrice F. Howitt and Miss Enid A. Larson typed preliminary and final versions of the manuscript.

Green-backed Goldfinch

Green-backed goldfinches (*Spinus psaltria* (Say)) live on open land, with a sparse cover of trees, and in brushland. The species occurs through a wide range of conditions of climate and weather. It is less plentiful in the humid coastal region. The land it occupies is mainly in the dry foothill regions and on the desert. Here is provided an abundant supply of seeds or

buds for food. The kinds of food eaten make it necessary that water be available in short flights. This finch probably seeks water more persistently than other members of its genus. Thickets of bushes or trees close to water are occupied consistently through the dry season. For nesting a great range of trees and bushes is used. Generally, the nest is in dense foliage and often it is toward the tip of a limb. Single birds in flight often perch at the topmost tip of the tallest tree in the vicinity. Common foraging places are in patches of weeds along roadsides, in pastures, and on slopes of hills.

In late August, 1931, a severe fire covered parts of Napa and Lake counties, California. This fire brought prominent effects on the bird populations in the region. Eight months after the fire H. W. Clark (1935) in mid-April went over a part of Bell's Canyon, two miles west of Angwin. A few black oaks and manzanitas survived the fire, and along the creek at the bottom of the canyon the alders and streamside shrubs were unharmed. The burned area was a mass of bloom. Many wild flowers had sprung up in profusion. Apparently the removing of the cover of brush had given them better conditions than usual. Green-backed goldfinches were the most abundant birds, supposedly because of the prevalence of seed-bearing plants.

Green-backed goldfinches in the northern Sacramento valley are found most often in blue oaks. Other trees frequented are live oak, valley oak, sycamore, cottonwood, and willow. Sometimes the birds are in bushes such as buckbrush. Telephone wires furnish perches that are used often. In winter they are in flocks that feed in trees and, more frequently, in weed patches in unplowed fields (Grinnell, Dixon, and Linsdale, 1930:403).

Tyler (1913:76) indicated that in the Fresno area the green-backed goldfinch and the willow goldfinch require different environmental surroundings. While the latter became much more numerous as a result of the human settling in the country, the former, never especially numerous in this region, responded much less favorably to cultivation, and decreased in numbers, to some extent, between 1900 and 1910. When the region was given over largely to grain ranches, with occasional weed-grown, uncultivated areas here and there, this goldfinch found conditions much more to its liking and was more often to be met with. Wherever sunflower patches occur it is still to be found, and during the winter months it often associates with house finches, going about in large flocks. Probably much the same sort of food is sought by each of these species.

Green-backed goldfinches occur in small numbers in the Toyabe region of Nevada. Specimens were obtained on August 30, 1931, at Birch Creek, 7000 feet, and on June 14, 1930, and September 4, 1931, on Kingston Creek, 7300 and 6000 feet. Sight records of others were mainly along Kingston Creek, between 6000 and 7500 feet, and in June and July. Usually the birds were close to the creek in aspen, cottonwood, willow, piñon, choke cherry, or apple trees. Even into late June these birds occurred in small flocks rather than completely segregated pairs.

From the Lassen Peak region there is evidence of a post-nest season movement of green-backed goldfinches from lowland up into the higher mountains. In 1924, at Battle Creek Meadows on June 22, one was drinking water from a ditch. On June 16, 1927, one perched in the aspen in that locality, and

sang there, before resuming flight. In July individuals were often seen in that neighborhood (Grinnell, Dixon, and Linsdale, 1930:404).

Willett (1933:163) characterized the green-backed goldfinch as an abundant summer resident in southwestern California from mesa and foothill regions to about 3000 feet in mountain canyons, south to Lower California; less common in lower country and in higher mountains. Grinnell noted them as high as 6500 feet (nesting at 6400) in the San Bernardino Range, and Grinnell and Swarth found them at 6800 feet in the San Jacintos. In winter the birds were distributed in flocks over the whole lower country. In that area the species breeds most commonly from April to July, but sometimes considerably later.

Howell (1917:76) considered this goldfinch as rather rare on the islands off the coast of southern California. Small numbers were seen on Catalina in spring of different years and, one year, three pairs were seen the last of December. On Santa Cruz Island this bird has been recorded in April and November. Howell thought that the species was resident wherever it occurred on the islands. Pemberton (1928:147) reported these birds as common on Santa Rosa Island and a set of eggs was taken on April 2.

COURTSHIP

Courtship in the goldfinches involves several kinds of behavior. In the formation of pairs there is likely to be courtship song, courtship flight, song flight, and a canary-like song. Courtship feeding is important in maintenance of the bond. These elements resemble the ones observed by Stokes (1950:109) in his study of the American goldfinch (*Spinus tristis*). The species studied on the Hastings Reservation contrast, in several ways, with the calendar of activity exhibited in the eastern species.

In midmorning of January 29, 1945, on a slope of a hill on the Reservation one male was perching at the tip of the topmost twig of a 40-foot leafless valley oak. Turning first one way, then the other, he was uttering an almost continuous song. This was the first green-backed goldfinch that the observer had heard, or seen, singing that season. In the last week, or ten days, of January he heard snatches of songs intermingled with a variety of calls. Other green-backed goldfinches were uttering a variety of calls from near-by trees. The next calls and songs were being uttered on February 12. These were the first heard in the vicinity for two weeks. At 8:00 A.M. on February 7, 1938, two goldfinches (male and female) stood on a fence in a chamise patch and within a foot of each other. After a flight of 50 feet by the female with the male following closely the male caught up, and both birds dived over a ridge in a close, twisting flight. On March 23, 1941, a pair of green-backed goldfinches flew across a yard with the male in the lead and singing. In late March, goldfinches were observed frequently, apparently in pairs, scattered over the Reservation. On April 5, 1939, several pairs were in display flight along a creek in the morning.

On April 16, 1938, in the afternoon, several green-backed goldfinches were scattered with Lawrence goldfinches, in blue oaks and out in a field, mostly eating nutlets of fiddleneck. Part of their time was spent in courtship behavior. This was not clearly understood, but it included pursuits—appar-

ently of males by males—displays with feathers raised, tail spread and elevated and wings waved rapidly, and flights in which the bird moved slowly, but with the wings moving much more rapidly and widely than in the ordinary flight. This slow flight was usually part of a pursuit. Besides this there was much singing from perches in the trees. The day was partly cloudy, but warmer than for several weeks. On April 20 many goldfinches were scattered through the oak woods and about the fields. In the afternoon in the blue oaks then coming into leaf, a male was seen in courtship flight several times.

On May 11, 1939, the goldfinches were numerous along a flowing creek, attracted there by the water. They were mostly in pairs. Some pursuits were noted, and there were some display flights. A pair at 8:15 A.M. on May 21 was beside a creek. The male chased the other bird away. About 11:00 a male in this vicinity flew about in 50-foot, slow flights, calling, with wings and tail widely spread and revealing the full extent of the white. On May 21, 1940, there was a display flight of a male following two other individuals along a creek. At 8:15 A.M. on May 22, 1938, a pair was in the top of a valley oak. The female postured; then coition was performed. At 8:30 A.M. on May 23, 1939, a mixed flock with many Lawrence goldfinches, was feeding on fiddleneck. When disturbed, the birds flew to a small willow. Here there were several short pursuits of males by males, mostly of Lawrence. Once one drove a male green-backed goldfinch from his perch. On May 31, 1942, goldfinches were numerous and active among the blue oaks on top of a hill where nesting took place. There were many flight displays by males with fully spread wings. Many females were seen, apparently not yet on nests.

At 8:30 A.M. on May 24, 1939, observations were begun when no birds were in sight at a nest in the second day of construction. A light breeze was swaying the nest-limb, 3 or 4 inches at times. The sunshine was bright on the nest and the air was warm. Both birds returned at 8:53, the male 5 feet ahead of the female. The male went to the nest-tree 10 feet from the nest; the female went to the nest-limb 4 feet from the nest, and then to the nest. There was a mating flight at 8:55. The male was in a valley oak southeast of the nest-tree, and the female was in the nest-tree. The male was 8 feet above the female. When the male flew down toward the female, she flew up 2 feet toward him, and he mounted. Both birds fell to bushes 3 feet above the ground, the male seemingly always above. They fell 25 feet in 2 seconds. When the birds struck the bushes alongside the road, they separated. The female flew into the bushes. The male, behind by 2 feet, followed the female around through the bushes under the nest-tree. The female flew to an oak, 20 feet southeast of the nest-tree. The male flew at the female twice from 5 feet away and the female flew off. She was either foraging or seeking nesting material. She flew back to the nest-tree after 1 minute in the oak. The male followed, 10 feet behind. Both birds went out of sight in the trees. The female flew east from the nest-tree after 30 seconds, the male behind by 20 feet. Both were out of sight in valley oaks, east of the nest. No singing was heard from the male. This mating was at a time when the air was warm and sunny, and there was little breeze. The pair returned at 9:15, the female 10 feet ahead of the male. She went to the nest, he to the nest-tree. At 9:20 the female was working on the nest, the male dived from the southeast oak below the

nest, and flew up again 6 feet from it, but not to it. Both birds flew away and the male pursued the female 6 feet from her perch, high in the tree. Later, the female flew to the nest from this direction. The male followed her 15 feet behind as she left.

Attention was attracted especially to the high flights of the males with wings and tails widely spread, revealing the contrasting pattern of white and dark markings to a full extent. This display is conspicuous as the males fly out in circles near the perched females. At 11:45 A.M. on June 7 a male was flying in circles 35 feet in diameter, 10 feet up, around a female perched on a barbed wire fence. The male spread his tail and fluttered in flight. He uttered a continual series of *dee-dee* notes and snatches of song. The female appeared to be entirely unaware of the performance. The female flew off and the male followed, singing and calling. At noon on June 16 ten goldfinches along a creek were in pairs and the males were singing. One male was flying in circles around the female perched on a twig 3 feet from the ground, seemingly oblivious to her mate's display. Several others were flying and uttering plaintive *tee* notes.

At 9:10 A.M. on June 17, 1948, a male was in a dense stand of live oaks on the floor and sides of a canyon. He perched in one tree top and flew out four times over the lower trees, circling once and singing an intense song compared to the light, whistling notes of ordinary singing. After each flight he paused in the tree tops 60 feet above the ground and sang in a leisurely manner. One or two birds uttered occasional notes from adjacent trees during this time; then one flew up from the top of a tree over which the male had flown and a chase ensued around a half circle for 200 feet among the tree tops. The second bird disappeared and the male, calling softly, perched for 20 seconds at the top of a live oak 75 feet from his original perch. He then flew off down the canyon. The second bird was probably a female. Apparently a courtship display had taken place among the tree tops. Birds were seen singly or in twos in the canyon through the morning. In the morning on June 28, 1938, several goldfinches were along a lane. At 10:30 a male was flying in circles and singing on the wing around a female perched below him in a coffeeberry bush. In early afternoon on July 14, 1939, a female perched 40 feet up in a valley oak. A male perched 3 feet above her and sang for 2 minutes and then he flew in two wide circles over a ravine in front of her, showing flashes of the conspicuous white wing patches. The male then perched alongside the female. This was a seasonally late example of this type of display.

NESTING

Dawson (1923:195) wrote that

the range of choice in nesting sites for [the green-backed] goldfinch is very great. Sycamore trees are an early favorite, because of the shelter promised by its generous leaves. And in this connection it may be well to note that most birds, whether ground or tree nesters, see to it that their nest is in shadow throughout the middle of the day. The burning rays of the sun must be avoided, at least by the tender nestlings. It is this fact, and not presumed escape from observation, which is the controlling factor in most nest-building projects. The cypress is also a favorite with the goldfinch, and whether the nests be placed close to the trunk of the tree, or, preferably, well out toward the tip of a branch, is determined again by the shade offered by some overshadowing twig or branch. Live

oaks conceal their myriads also. In this case, the bird, securely sheltered by a bristling array of sturdy leaves, prefers the tip of a drooping branch, or at least an outside situation. When the timber gives out, the Greenbacks take cheerfully to the major weed-patches, or even invade the open sage, to take pot luck with Bell Sparrows and Bush-Tits.

In the fourth week of April, 1928, several pairs of green-backed goldfinches were nesting among the blue oaks on the hills 6 miles north of Red Bluff. An unfinished nest was in a shrubby tree at the edge of a small clump. The nest was 5 feet up on a limb sloping at a 45-degree angle and near the center of the shrub. The female kept up a twittering call as she shaped the nest that was made almost entirely of sheep's wool. Another nest in the same region, on June 12, was 4½ feet up in terminal foliage of an oak. The nest was built of plant fibers and was lined with wool, fibers from cottonwood seeds, rabbit-fur, and horsehair. (Grinnell, Dixon, and Linsdale, 1930:404).

In February, near Whittier, E. M. Hall (1938) watched a green-backed goldfinch removing the nesting material from a Hutton vireo's nest and placing it in the goldfinch's nest in a near-by tree.

On the Hastings Reservation several times we have seen goldfinches taking nesting material from nests of the Bullock oriole. Late in March a female flew to an old oriole nest where a male joined her. They proceeded to pull bits of fibers from the outer surface of the nest. The male pulled out a 6-inch long fiber, but he did not take it away when he flew to another part of the tree. The female pulled bits of fluffy material out of the nest, but she did not take it from the site when she moved elsewhere in the tree.

On June 22 a pair of goldfinches at midday perched only 7 inches from an oriole nest containing 10-day old young. The female goldfinch hopped to the side of the nest and pulled fibers from the rim to a place 3 inches down the side. After about six such tugs the female had a billful of fibers and both members of the pair flew off, presumably to their nest. The next day the female was back and the performance was repeated.

At Point Lobos in 1934-35 the only nest of green-backed goldfinch found was 8½ feet up, at the end of a bough of a 20-foot Monterey pine. The limb was at the south margin of the woods on the north side of a meadow. The site was thus open to the south and west, but pines stood close on the east, and they provided shade in the morning. On April 26 the female was at the nest, which we thought then to be empty, and the male was near it. The male flew, singing in slow flight, to the top of a dead pine 50 feet from the nest. The female was still brooding on May 11 (Grinnell and Linsdale, 1936:122).

At Mecca, at the north end of Salton Sea, March 18 to 31, 1911, several pairs had nests well underway by March 30; thread and cotton from the skinning table went into their makeup (van Rossem, 1911).

Nest building begins in Santa Clara County in early April (March 30, 1889), and fresh eggs may be found as late as the first of August (July 31, 1888). The number of eggs laid varies from three to five, but usually is four. Rarely, sets of pure white eggs are found. One egg of a set of four of the usual bluish tint, was finely dotted with reddish brown. The nests in this area are built in all sorts of trees and bushes (blackberry, raspberry, grape, maple, orange, apple, peach, oak, fig, bay, greasewood, and bamboo), at heights varying from 2 to 30 feet (van Denburgh, 1899:170).

Green-backed goldfinches in central Lower California were recorded by Bancroft (1930) only from San Ignacio. The birds were common in the gardens near the reservoir, where they began to nest the first week in April. They build with plant down and the finest bark. They place their nests, by preference, in the grapevines, though it is by no means unusual to find them in willow or fig trees. The nests were hidden by especially timid birds. With the exception of one set of five, all the clutches had three eggs.

Nests in California are usually in bushes or trees in fairly dense foliage, from 2 to 30 feet above the ground. Some sites used were in the following plants: cottonwood, grapevines, willow, fig, pear, apricot, lemon, live oak, arrowweed, blue oak, walnut, boxelder, blue gum, and cypress.

On the Hastings Reservation there is prominent variability in the numbers of goldfinches that nest and in the time of year in which they nest. Nest building may begin late in March elsewhere in central California. Our earliest record indicating attachment for nesting was on April 11. In the area early nests are likely to be deserted because of spring storms or prolonged cold weather. When this happens the birds wander from the first site and start nesting anew when the weather improves.

Observers on the Hastings Reservation have kept full records of the nesting of goldfinches, especially at nests that could be watched with a minimum of disturbance of the nests and the birds. This information pertains mainly to the behavior of the birds. The observations were continued through as many hours and days as conditions permitted. Study away from the nest was undertaken also.

On April 11, 1939, several pairs of goldfinches were in a canyon. One pair seemed especially attached to a site for nesting in a clump of lichen (*Ramalina reticulata*) 7 feet up at the end of a branch of blue oak. The female went there half a dozen times in about an hour and then the male usually perched about 10 feet off. No material was seen. The birds were excited by the near approach of a pair of house finches.

On April 20 a pair of goldfinches was building a nest in a heavy cluster of lichen hanging from the lower end of a blue oak limb only 4 feet above the ground about 15 feet from a house finch's nest and upslope from a Hutton vireo's nest. The female carried all the material, which was mostly gathered within 50 feet of the nest; sometimes she was accompanied by the male and he watched her from a perch 6 feet away. The male took no part in a prolonged fight between the female and a female of a pair of Lawrence goldfinches which came into the nesting tree or in the more vigorous attempt by the female to drive away an intruding female house finch from a nest in an adjacent tree.

On April 24, 1946, a nest was in the process of construction about 15 feet above the ground in the outer branches of a live oak at the edge of a clearing beside a creek. A female was placing small bits of dead grass on the outside of the nearly completed nest. As far as could be seen it was made entirely of dried grass.

On April 29, 1939, among several goldfinches along a creek one female was building a nest in dense foliage 20 feet up in the top of a small live oak.

On May 11 a female goldfinch flushed from a nest 7 feet up in a 9-foot

blue oak halfway up the south side of a hill. The bird stayed within an area 50 feet across, moving from tree to tree and uttering single, loud notes of alarm. The nest had slight, whitish walls so thin in places as to let light through. It contained 4 eggs. The lining was dark. The bird became quiet in 3 minutes. The rocky ground was covered with slender oat. The tree was near to a small dead one. The other blue oaks were 10 to 60 feet away. The site was exposed and a cold wind was blowing.

On May 13, 1941, a female was building a nest 20 feet up in a clump of lichen in the drooping limb of a sycamore close to a creek. The builder made three visits to the nest and other trips to lower levels for material. The day was cloudy after rain. On May 13, 1943, a female was building a nest in lichen 30 feet above the ground in the tip of a slender blue oak. On May 17, 1939, a nest in a blue oak with trunk 5 inches in diameter was on the south slope of a hill. The female was flushed from the nest 7 feet above the ground on a branch 11/2 inches in diameter and semi-sheltered over the top by leaves. The hillside was steep and rocky. The vegetation was slender oat, blue oak, and chamise. The nest held four eggs. The trunk of the tree holding the nest was 5 inches in diameter. On May 19, 1941, a few goldfinches were at the site of a nesting colony, of other years, on the northeast side of a hill and these stopped only momentarily or flew overhead. However, many were present later in the morning in a field at the top of the hill in valley oaks and were flying down to perch on fiddle-neck stalks and to eat the ripening nutlets. The next day, 50 feet upslope from a creek, a female was building a nest. At 9:15 A.M. on May 22 a male repeatedly came to the tree and perched close to the nest. The site was a foot below the top of a slender 15-foot live oak, at a lower level and within 20 feet of nests of Anna hummingbird and black-headed grosbeak on the same slope. It was overtopped and shaded by tall valley oaks and live oaks. At midmorning on May 23, 1939, along a lane a female carried material six times to the end of a limb where a nest was barely begun near the top of an upright limb 45 feet aboveground in an open cluster of valley oak leaves. The male accompanied the female and sang from a near-by perch, usually below the nest. The trips were soon discontinued. At 9:30 A.M. on May 29, 1938, a female was carrying nesting material, gathered in a live oak, to a nearly completed nest in the end of a bough 30 feet up in a big-leaf maple beside a small stream. The male was singing in the vicinity.

At 9:00 A.M. on June 3, 1941, a goldfinch was beside a road gathering cottony material and shreds from a dead plant. At 9:00 A.M. on June 8 a female flew off a nest in a three-way fork of a 1 1/4 inch stem of red willow 25 feet above a creek. It was on the southeast side of the stem and exposed to the northeast. It was shaded and concealed from the south, west, and north by tall live oaks. At 9:05 the female was fed by the male. She quivered her wings whenever the male was near. The male went into the nest to feed the female.

At 11:30 A.M. on July 2, 1948, a female was carrying material to a nest less than one-fourth completed in a hanging cluster of leaves a little over 7 feet above the ground on the west side of a valley oak near a barn. The bird gathered shreds of bark from stems of plants inside a willow clump 100 feet

away. On July 12 the female was incubating. The observer walked within 5 feet twice without causing the bird to leave.

On July 17 this nest appeared unattended at 8:20 A.M. The foliage cluster among twigs made difficulty in seeing the nest. When an observer touched the limb, however, the female leaped out and fluttered to bare ground 12 feet away, along the northeast end of a barn. She turned, watched for 2 or 3 seconds, and then fluttered off, barely clearing the ground, to and around the east corner of the barn. Her body in flight was held slanting forward at 75 degrees above horizontal. The tail seemed to be spread as a brake to intensify the effect of the fluttering motion. The display was remarkably similar to that of a female lazuli bunting. The chief difference was that the goldfinch was silent.

At 11:00 A.M. on July 23, the nest contained a young bird, 1 to 2 days old. The female was brooding, but she did not leave until a mirror was held over the nest. Then she fluttered off the nest and to the northeast. After reaching the tops of the dead grass at a point 14 feet from the nest she fluttered, turning from side to side, over a path 3 feet wide for an additional 10 feet and then flew 30 feet from the nest to a hanging branch and perched, calling a series of slow *kiyah*, *chee-wee*, and *chee* notes. In 3 or 4 minutes she gradually worked back to a point 10 feet from the nest and 15 feet above it. She remained there calling, as long as the observer remained at the nest, an additional 6 or 8 minutes.

At 10:55 A.M. on July 29 the female was brooding when the nest was examined. She flew off in a long, fluttering glide for 40 feet, alighted, and then went around the east corner of the barn. Her retreat was much quicker than when incubating. The female returned immediately to a tree 10 to 20 feet from the nest calling *tee-ah* and *hee-wee* notes.

Nesting season.—In the San Francisco Bay Region the normal nesting season extends from the last of March to the last of July, with an unusually late nesting date on November 2, at Berkeley (J. Grinnell and M. W. Wythe, 1927:110). Grinnell (1914a:165) on March 25, 1910, found two partly constructed nests in the vicinity of Ehrenberg, Arizona. The sites were 4 feet above the ground in arrowweeds.

In the Providence Mountains in southeastern California, this bird was nesting in late May and early June, 1938. On May 20 many individuals were singing and one was carrying nesting material. A male on May 30 had testes 6 mm long and a female on June 9 had slightly enlarged ova (Johnson *et al.*, 1948).

At Escondido, on September 24, 1908, C. S. Sharp took a set of four eggs being incubated. At Santa Fe, New Mexico, in 1921, Jensen found 22 pairs nesting on the campus of the Indian School, and he found fresh eggs from June 15 to October 1 (Bailey, 1928). At Limpia Ranch in the Davis Mountains of Texas on September 19, 1907, Austin Paul Smith saw fledgling goldfinches barely able to fly. In California at Simi, Ventura County, Appleton (1916:30) on October 22, 1915, found a female brooding three eggs. The eggs hatched on October 24, and the nestlings were still in the nest on November 4, but they had disappeared by the 8th. Peyton (1911) found a nest on October 23, 1910, with four nearly grown young at Sespe. The

young left the nest on October 29. He cited another nest found by Harold Pyle on October 26 with four young that fledged on November 8. In southern California on October 31, 1925, Clinton G. Abbott saw a female feeding young still in the nest at the San Diego Mission.

On November 18, 1952, in Oakland, Mrs. H. K. Trousdale watched a green-backed goldfinch feeding fully fledged young. Miller (1903) found a nest containing four fresh eggs on November 22, 1900, at Parlier, Fresno County. A week later the nest was destroyed by several days of hard rain. A late nest in southern California on November 1, 1921, contained two fledglings that departed the next day. At Escondido on November 4, 1918, Carpenter (1923) found a nest 8 feet above the ground. It contained two partly feathered young.

Nest building.—A pair of goldfinches was building a nest on the Reservation in a valley oak on May 23, 1939. The nest was in direct sunlight on the northeast side of the tree and it swayed violently in the wind. Shortly after 9:00 A.M. the birds made two or three trips to the nest-limb. At least once the male perched on a bare twig 2 inches below the nest. The pair returned at 9:43; the male went to the nest first, carrying material. He did not remain at the nest. The female came to the nest and worked 2½ minutes while the male remained near the center of the tree. He carried the material until the female left; then he brought it to the nest and worked half a minute. Both went away. When the female returned and stayed 15 seconds, the male did not come near the nest, but he remained 10 feet below it in the tree. The female then flew down into the tree and both flew out, one pursuing the other through a live oak east of the nest and back through the nest-tree. The female again went to the nest from the north for 15 seconds at 9:49.

The male was not seen. He had flown south through the nest-tree. At 9:57 the female came to the limb near the nest, then to the nest. The male went into the crown of the tree, not near the nest, and remained 15 seconds. At 9:59 the female came again from the north. She was in the nest 15 seconds, then into the tree and at 10:00 the male came to the nest from the north for 30 seconds. He was weaving fiber around twigs 3 inches above a fork of twigs. Sometimes he flew directly to the nest, sometimes to a branch south of the nest. Once he appeared to climb up to the nest from below, using his bill parrot-fashion. The female came to the nest at 10:05 and remained 15 seconds; then she flew into the nest-tree, vigorously shaking the twigs above the nest. At 10:06 the female was at the nest. She made visits at 10:07, 10:08, 10:08½, and she was on the nest at 10:09 and 10:10 A.M., for 10 seconds the last time. She was getting material out of the live oaks. At 10:11 the female was at the nest for 15 seconds, then into the nest-tree. At 10:12 she flew from the nest-tree for 15 seconds, then back into the tree. At 10:14 the female flew from there and back to the nest-tree in 45 seconds. At 10:17 she came from the south and circled the nest. She went into the top of a live oak to the west and then back to the nest. She was at the nest 30 seconds, then into the nest-tree, and back on the nest again at 10:18. The male was below on a bare twig. In 15 seconds, both flew up the hill. At 10:20 the female came to the nest from the southeast, but

brought nothing. The male was waiting in the nest-tree. The female was in the nest 10 seconds, then flew west to a live oak. At 10:22 the male was in the crown of the tree, but he did not see the female. She was not at the nest.

The male had been at the nest only once so far, but the observer may have missed some trips. The female came back from the west at 10:29, remained 45 seconds, then flew west. Again she returned for 15 seconds at 10:30 from a live oak in the east. She flew west, returned at 10:32, for 10 seconds, without material. At 10:33 she brought material and remained 1 minute, weaving. She was there at 10:35 for 5 seconds, at 10:36 for 10 seconds; then she went from the nest-tree to an oak in the west. At 10:37 the female went from and to the west oak in 10 seconds. Probably she brought cobwebs. The male went from and to the west oak and worked 10 seconds. At 10:41 the female made another trip. At 10:43 she came to the nest-tree. The male came near her from the north. The female was on at 10:44 for 30 seconds, but the male remained where he was. Both flew away east out of sight, the male after the female, zigzagging through the crown of the live oak, the male 18 inches behind the female. At 10:50 a heavy breeze blew one piece of material out of the nest. The male sang near by sometimes when the female was working. She did almost all the work.

Most of the material came from the near-by trees. The nest then had a thin base 2 inches wide by 3 inches long. Most of the time the female flew directly to the nest from a near-by tree, but if she came from farther away, she generally lit in the nest-tree and then went to the nest. She returned at 11:37 from the north. The male flew to a branch near the nest, the female was farther away. The latter went to the nest, while the male was near by. He was not at the nest and carried nothing; neither did the female have anything. She was at the nest 40 seconds, but the male moved away. The female was on at 11:38, when the male came back to the nest. At 11:40 the female flew away. She returned, but the male flew before she arrived. The female was on at 11:41 for 30 seconds and again for 15 seconds. She was getting nest material from the nest-tree. At 11:40 the male worked at the bottom of the nest from below. This was in the parrot-fashion previously referred to. At 11:45 the female came to the nest from the south for 15 seconds, then flew east. The male was not seen after 11:45.

Two hours and 40 minutes were spent at the nest by the observer. The male made 5 trips to the nest and the female made 33. For the female the average interval between trips was 4.9 minutes.

At 1:45 P.M. material had been added to the nest since the observer left. When the birds arrived, both went to the nest, the male below, the female above, in the nest. The male went to a branch south of the nest, the female stayed a while; the male returned, and the female flew away. The nest swayed far out as the limb swung, but the birds continued to work on it. When both were on the limb, the nest bent considerably. It then was sunlit. The male generally quivered the wings when near the nest or the female. At 2:58 the male arrived first, and lit near the nest. The female flew up and the male flew to a branch next to the nest. The birds did not work much in the afternoon. The female returned to the nest at 3:37, but the observer

could not see the male, which did not come near the nest. The work was sporadic. The female flew to the nest site and possibly she arranged fibers; then she flew away. Perhaps the stimulus for building was not yet strong. At 3:43 the male and female returned together, but the female went to the nest, the male came only to the nest-tree, and then moved away.

About 3:50 P.M. the female resumed work on the nest, and she spent longer periods there. The observer could not see whether she had brought material, but at every trip she would work at the nest, twisting her head from side to side. At 4:02 she flew to a live oak 15 feet from the nest; there she pecked at the base of a dead branch, among the lichens. She seemed to work at a tree for awhile and then change to another. Generally she went to the same place in the tree. The male was not seen near the nest after 3:43. He had evidently ceased working. At 4:30 a pair flew into a live oak 15 feet southeast of the nest, but they moved to the west, not stopping in the nest-tree. The female shook her wings up and down before the male. The nest-building female made 29 trips to the nest. In the afternoon, the male made one trip in 3 hours. For the female the average interval between trips was 6.2 minutes. The observer returned at 5:30 p.m. and waited until 5:35, but he saw no birds near the nest.

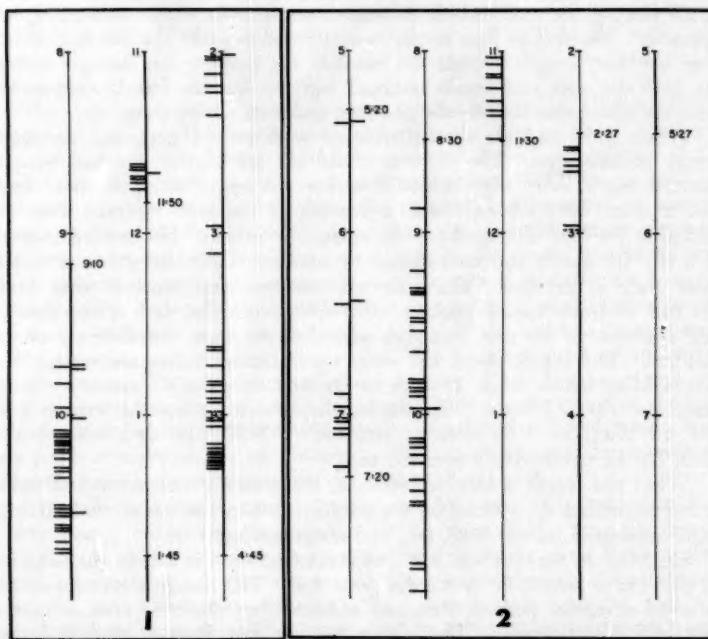
When the female worked at the nest, she generally was above and inside it, but sometimes she worked on the outside. When she was at the nest, one could sometimes see the head, tail, and wings moving.

On May 24 the nest was still under construction. It was in the sunshine all day, but it swayed in the wind a great deal. The female almost invariably followed a regular path to the nest, at least when the wind blew from the west as it did normally. She approached the nest from a perch 6 inches below and from the southeast. The male seemed to stay in the sunshine in the vicinity more than the female did. The female worked part time at the nest when it was in the shade.

Toward the end of the morning the wind increased. The female stayed in the nest for 4½ minutes as the wind held the limb in a horizontal position. Even though the nest was kept on its side the bird remained in it. The nest position was changed in this manner three times while the wind was strong. Once when the female came to the nest, the wind was swaying it so hard that she had difficulty in alighting. She swerved around the nest and attempted to alight headed into the wind. At that moment the nest swung out of position and the bird missed the rim. She fluttered for a second, and when the wind moved the nest back to her, she clutched the rim, fluttering her wings to keep balanced, and got into the nest.

In midafternoon the female made three trips to the nest-branch, but she stayed at least 4 feet from the nest. She was searching for material, but she took none to the nest. The branch was well covered with lichen (*Ramalina*), but the plants were mainly small ones, about 2 inches long. The bird sought plants that were at least 6 inches long.

On May 24 in early nest-building stage the male exhibited several traits of behavior as he accompanied the female on trips with material. Once he flew past the nest-tree and turned back to it as the female went straight to the nest. The male remained on a level with the nest, but he moved about as the



Figs. 1, 2.—Nest construction by pair of green-backed goldfinches. Marks to left of each column indicate trips by female with material; marks to right indicate trips by male. 1. May 23, 1939. Observations from 9:10 to 11:50 A.M. and 1:45 to 4:45 P.M. 2. May 24, 1939. Observation from 5:20 to 7:20, 8:30 to 11:30 A.M., and 2:27 to 5:27 P.M.

female worked. The male continuously jerked his tail and wings as he perched. For 10 minutes the male remained in the top of the nest-tree, moving from place to place, about 15 feet from the nest. He pursued a male and a female of his species when they came near the nest-tree, but he came no nearer than 1 foot from them.

On the second day of nest building the observer recorded activity through four periods: 2 hours in early morning; 3 hours before noon; 3 hours in early afternoon; 81 minutes in late afternoon. In this time the female made 64 trips to the nest and the male made four trips. In early morning the average interval between trips was 13 minutes for the female and the male made trips 60 minutes apart. In late morning the intervals averaged 5 minutes for the female. In the afternoon the intervals averaged 25.5 minutes for the female. In the late evening the intervals averaged 6.8 minutes for the female.

The female was hunting for lichens to add to the nest. She twice pulled vigorously at one plant 6 feet above the ground, but she did not obtain it. Three times in 10 seconds she returned to the same place and worked at the side of one clump. She worked for 6 minutes about a clump and could not

break off pieces. She hopped in and out, hung upside down, pulled at least ten pieces and pecked at others before returning to the nest-tree.

This nest was destroyed by scrub jays (*Aphelocoma coerulescens*) soon after the construction was completed.

INCUBATION PERIOD

Chambers (1915) traced the history of a green-backed goldfinch's nest in southern California in April 1915. The nest was started on April 4 in a lemon tree where the pair had been present for several days. The nest was nearly completed by the 11th, and there was a lining of feathers. On the 17th at 6:00 A.M. the nest contained the full set of four eggs and at 6:30 A.M. on April 29 all four eggs had hatched. The incubation period, then, would be twelve days. Gross (1938) reported this as the incubation period for the American goldfinch.

INCUBATION

In midmorning on June 6, 1939, a female made three trips to a nearly completed nest 30 feet up in the top of a live oak limb. Once the male followed and perched quietly 10 feet away from, and below, the nest. When the male did not accompany the female, she kept up a constant chatter, heard easily 80 feet away. The female turned to the right in the nest and worked at the rim and on the outside. The trips were made downhill. At 11:45 A.M. on June 8 a female was on a nest in a live oak. A male had been in the tree at 8:30 A.M. At 2:45 P.M. the nest was not attended. After an absence, the female went to the nest and the male flew out of the tree. The female in the nest was squirming and working at the rim with her bill. She did not rotate in the nest, but after 3 minutes she became still and remained so until 3:10. Incubation had begun. At 5:40 P.M. no bird was on or near the nest.

When the observer arrived at 5:00 A.M. on June 10, no bird was on or near the nest in the live oak. At 5:42 the male and the female flew up the ravine from the northwest. The male stopped in a valley oak 40 feet north of the nest-tree; the female flew to a perch 1 foot from the nest and entered facing southeast. She remained quiet, without adjusting the rim. The male did not sing, but after half a minute he flew. The female moved about somewhat in the nest, but she did no energetic preening. At 6:20 four Lawrence goldfinches were in a tree 100 feet from the nest, at the same time the female was sitting up in the nest looking toward them, restlessly. After the intruders flew east within 100 feet of the nest, the female got off, and flew 100 feet to a sunlit live oak where she paused $\frac{1}{4}$ minute; then she flew out of sight. At 6:43 the male and female returned from the direction of the water trough. The male stopped in a valley oak north of the nest. The female went to the nest, and faced toward the southeast with the tail projecting at a 10° angle above horizontal. The male left. At 6:58 the male came into the nest-tree. He worked up through the tree from 10 feet below the nest. The female began to flutter her wings (more than quivering of *S. lawrencei*) and reached up to the male when he came to the nest. The male stood a moment before feeding the female (longer than *S. lawrencei*). He then

worked down into the tree again, instead of flying out from the nest, which could have been done easily. The female wiped her bill on the near-by twig. She reached 2 inches to it, turned to face southwest in the nest, and became quiet. At 7:10 the sun was lighting the foliage 1 foot on either side of the nest, but the nest remained shaded; the only place in this leaf cluster that was shaded. At 7:15 A.M. the female was on the nest, quiet, and not preening as a *S. lawrencei* female had done.

On June 14 observations began at 5:00 A.M. at the nest. The female was incubating. She was quiet and motionless except for movements of the head, looking from side to side and down. At 5:30 the male came up through the nest-tree from 8 feet below the nest and moved up to it. The female fluttered her wings when the male came to the nest and fed her. Then after a pause of 1 second, he flew down into the tree 10 feet below and south of the nest. During the feeding the flash of wing-bars was not seen, but after feeding, when the male flew downward, the wings showed bars clearly. The female flew off the nest north to valley oaks 40 feet away, paused there $\frac{1}{4}$ minute, and flew toward a water trough.

The female returned directly to the nest 5 minutes later. She sat on the nest facing south until about 6:15, then turned to face southeast. She was still quiet, moving only her head. The sun was not yet on the nest. At 7:00 the breeze from the northwest swayed the nest-limb. After it stopped, the female turned to face northwest. The turning consisted of a series of short moves, without rising from the nest. At 7:15 the female was quiet on the nest, facing northwest, the sun striking the nest-branch, but it was generally obscured. At 8:17 the female was on the nest, facing northwest into the wind. When the wind swayed the nest, the female looked around nervously; otherwise she remained quiet. The sun was now on the nest. At 8:43 the female turned to face southeast although the wind was still from the northwest.

At 9:32 the male flew to a perch 10 feet below the nest. He remained there 1 minute, moving toward the nest by 3-foot long flights. When the male was 5 feet from the nest, the female began to flutter her wings and twitter. The male came to the nest and perched on the rim to feed the female. He stood erect to feed, as the female in the nest fluttered her wings hard. The female had turned to face the male to feed. He fed her for $\frac{1}{4}$

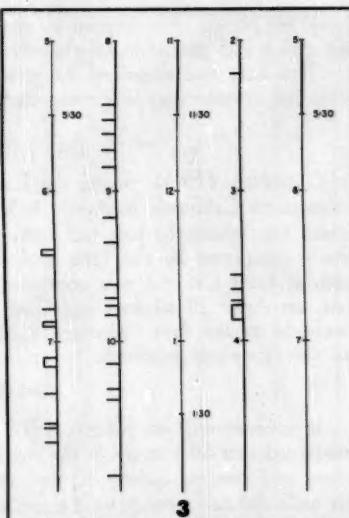


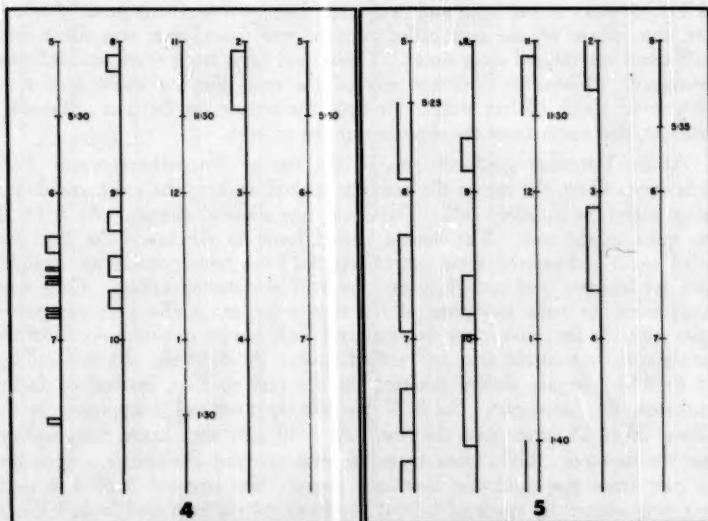
Fig. 3.—Visits to nest by female green-backed goldfinch, Aug. 4, 1941. Observation from 5:30 to 11:30 A.M. and 1:30 to 5:30 P.M.

minute and then flew to the original perch, where he paused to wipe his bill before flying north 80 feet to a bare branch in the top of a valley oak. Then he sang twice and left within 10 seconds. The female or male, or both, twittered on the nest.

At 9:58 A.M. on June 14 the female flew off the nest 50 feet to a live oak on the hillside, level with the nest. She remained there 10 seconds, out of sight, and then flew. Next, she went up to the nest from near the ground. She carried a grass stem with some seeds or heads on it, 4 feet over-all. This she worked into the rim of the nest. The female could leave the nest without a visit by the male.

Behavior at a late nest was recorded on August 7, 1941. This nest was in a sycamore and it was about 15 feet above the center of a road. The nest blended well with the sycamore bark and it was partly concealed on every side by the green sycamore leaves. Greenish yellow leaves lodged on the limb close to the nest and dark shadows blended with the black and dark green colors of the male when he brought food to the female and the nestling. Late in the morning the young bird stood on the rim of the nest and uttered a high-pitched chatter. The male brought food which he delivered to the nestling with 7 or 8 bobs of his bill. His stay at the nest was no longer than 3 or 4 seconds.

The one young bird in the nest showed no traces of down from a place 10 feet away. The nestling was plain brown above with no noticeable markings on the head, back, or wings. The edge of the nest was clean, with



Figs. 4, 5.—Periods on nest by female green-backed goldfinch. 4. Aug. 5, 1941. Observation from 5:30 to 11:30 A.M. and 2:00 to 5:30 P.M. 5. Aug. 6, 1941. Observation from 5:25 to 11:30 A.M. and 1:40 to 5:35 P.M.

no droppings visible. The west edge of the nest was the lowest part of the rim and it was used the most by the adults when they entered or left the nest. An automobile that passed by the nest created so much wind that the young goldfinch opened its mouth and started to spread its wings as the branch sank. The same behavior was noticed two minutes later when a large truck went past.

When the female was on the nest, she was above, and slightly to one side of, the nestling. There was no room for both of them in the bottom of the nest. When the male came to the nest, he approached from the same direction; at least the last 10 feet was over the same path. He perched on the same twigs prior to reaching the nest rim. He left as soon as he had finished feeding the birds in the nest and, always, he gave three or four even-notes which were lower in pitch than the two-parted call he used before coming to the nest. When the female left the nest, she left in the same direction that the male did. She also uttered notes at the beginning of her flight.

On August 13 at another nest in a sycamore when the female came to the nest in early morning, she spread her wings and ruffled her body feathers, sitting high, and plainly visible on the nest. At 6:37 A.M. the male approached the nest from the upper parts of the nest-tree. He paused on a twig about the same height as the nest and 8 to 10 inches from it. He perched on the west rim while he fed the bird in the nest, but he left from the east rim, going northeast through the tree. When the male called less than 15 feet from the nest, the bird in the nest responded with a musical chatter. A female appeared on a branch 2 feet from the nest. She looked about with quick jerks of her head and body and then went onto the nest. At 7:48 A.M. the female on the nest called four or five times, then was silent until 8:05 when she uttered three notes. These were wiry, two-parted, and inflected downward. When the bird first entered the nest, she was easily seen from the ground about 20 feet away. At 8:07 the female on the nest answered a faint call that came from the direction of the willows.

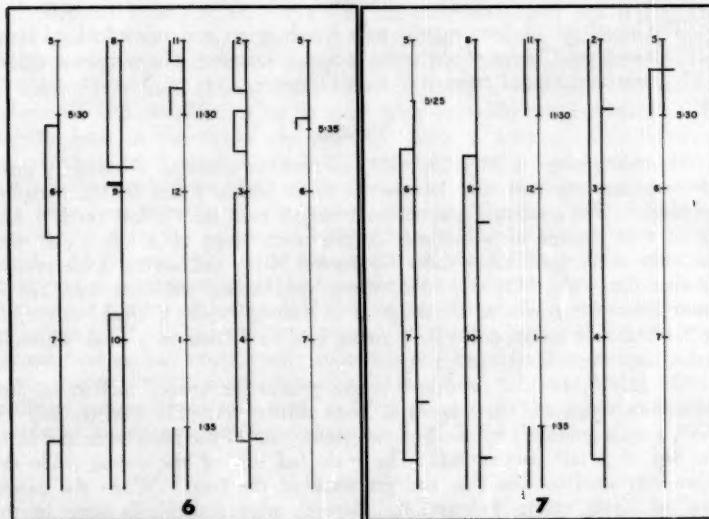
At 8:10 another goldfinch was in the top of the nest-sycamore. Both birds were calling, the one in the nest was excited, making the most sound, and rising slightly with every call. There was one musical chatter. At 8:14 all was quiet in the tree. The female settled lower in the nest. At 8:22 she called again and uttered three notes. At 8:25 the female stood up, straightened her feathers, and settled again. At 8:27 she started calling. Calls were heard from the oaks southwest of the nest-sycamore. Calls were two-parted notes with the last part lower in pitch and with a wiry quality. At 8:30 the female stood up on the nest and settled again. At 8:35 she was still calling. At 8:36 the female shifted position on the nest so that, instead of facing southwest, she faced east. At 8:37 she left the nest and disappeared in the willows 20 to 25 yards from the nest. At 8:49 calls were heard from willows near the nest-tree. Calls came from the nest-tree and the female approached the nest from the southwest side and above. She stopped 3 or 4 seconds on a twig within the space of 1 foot, southwest of the nest and looked about. She entered the nest from the east.

At 9:00 A.M. the female stood up on the nest, her tail and wings quivering violently and made a loud chatter. This continued for about 1½ minutes

with short pauses no longer than 1 second. All this time her tail was extended over the edge of the nest. When she stopped chattering and quivering, she stood on the edge of the nest. She then settled back on the nest with her tail up at an angle of about 60° above the nest. Earlier in the morning her tail was straight out and slightly down from the nest rim. She gave two two-parted notes. At 9:50 the female went to the nest after pausing on the twig only long enough to utter the notes. There she sat high and looked in all directions with short, quick jerks of the head. At 2:25 P.M. the female in flight appeared over the hill, above the trees bordering a creek. She apparently was alone and entered the tree through its crown. She kept her altitude until she was nearly to the tree and then dropped rapidly. She appeared on a twig 3 feet above the nest from which she hopped to a twig below the nest and finally settled.

At 2:46 she preened her back. At 2:48 she extended her left wing slowly, spread the primaries so that each one could be seen separately, and closed them. She returned the wing to a normal position close to the body. At 2:50 the female shook her head rapidly to the right and left in a quivering motion.

Soon after 7:00 A.M. on August 14, the male fed the female on the nest. Before his arrival the female uttered a soft, high-pitched chatter and quivered her wings. The male stood on the rim of the nest and made 33 deliberate feeding motions. For 2 minutes after the male left, the female kept up a constant, high chatter. Two minutes later she stood up and left the nest.



Figs. 6, 7.—Periods on nest by female green-backed goldfinch in incubation. On right of the columns are indicated two (fig. 6) and five (fig. 7) trips to nest by male. 6. Observation from 5:30 to 11:20 A.M. and 1:35 to 5:35 P.M. 7. Observation from 5:25 to 11:30 A.M. and 1:35 to 5:35 P.M.

The female on the nest was alert to everything that went on. Whenever a scrub jay called in the vicinity, her head turned sharply in that direction. She seemed aware of the observer's activity, but she was not unduly excited by it. As she covered the nest, she did so with a rapid cradle-like sidewise rocking of her body. At 8:21 she stood on the rim. Everytime she stood up, she also worked quickly with her bill in the bottom of the nest. At midday the female returned to the nest. She called nine times in the tree before she reached the nest. She moved from perch to perch ten times in moving down through the tree to the nest.

At 10:37 A.M. the male came to the nest through the top of the tree. He fed the female and uttered calls during his stay. The female appeared to arch her back and flutter her wings as the male fed her. Once a small white object was seen on the bill of the male. After he left, the female made cleaning motions with her bill, and she stopped fluttering.

After the male left the nest, the female kept up a constant high-pitched, excited chatter. This was accompanied by a fluttering of the wings. When the male left the nest, he flew much closer to the ground than did the female. He dipped to within 7 feet of the ground while the female stayed 9 or 10 feet above the ground when leaving the nest. The male returned to the tree from the north, flying into it 3 or 4 feet above the level of the nest. The female called before she went onto the nest and then was silent. She faced west for one minute and then turned south in the usual position.

EGGS

The usual set of four eggs is pale bluish green and unmarked. Hanna (1924) weighed 27 eggs of the green-backed goldfinch. The weights averaged 1.05 grams and ranged from 0.87 to 1.15 grams.

YOUNG

In midmorning on May 23, 1938, an observer watching a blue-gray gnatcatcher's nest reported that he saw an adult female junco feed a fledgling goldfinch. The goldfinch gave strident hunger calls from a low perch 1 foot up in thick foliage of a live oak on the north slope of a hill. The man had seen adult goldfinches there for several days, and several were present on that day. On May 31, 1946, young goldfinches, out of a nest, fed in association with adults at the edge of a clearing beside a creek. On July 1, 1939, a male accompanied by a young bird flew down to a creek where he bathed and immediately flew away.

On July 9, 1941, a family of young goldfinches uttered high calls, fluttered their wings, and ate achenes of Napa thistle. At 9:15 A.M. on July 11, 1939, a male goldfinch followed by two young, out of the nest, came and lit in the top of a tall cottonwood. The male fed one of the young while the other attempted to crowd in and get some of the food. When the parent flew off, both young followed it. Several other individuals were in the vicinity. There were two types of calls. Near noon on July 16, 1948, a family of young goldfinches was in an alder tree. One young bird, begging for food, followed an adult female and was fed. Ten feet higher in the tree another young begged from a male. The birds moved into the willows and

3 minutes later six of them flew up from there and moved to a lower group. One was begging for food as it flew, uttering a high-pitched and plaintive *twee*. In early morning on July 20, 1942, a female goldfinch accompanied two young, begging for food, in black sage. The young birds crouched and shook their wings. At 11:00 A.M. on July 23, 1948, the young bird on the nest was able to raise its head to beg for food; its eyes were closed and the feather tracts were represented by a grayish, light-colored down. The adult male did not appear. At 10:55 A.M. on July 29, 1948, the young bird in the nest showed pinfeathers on the wings, the eyes remained closed. At 6:10 A.M. on July 31, a family of goldfinches was in a buckeye. The young were being fed; at least they were begging with faint cries and quivering wings. The parent was foraging in the tree and on the ground beside the creek where *Polypogon* and other grasses were growing.

On August 1, 1939, there were feeding calls; then an adult female flew from a nest 35 feet up in the end of a limb on the southeast side of a live oak. At least one bird, not yet able to fly, was clinging to twigs beside the nest. At a nest watched on August 7, 1941, the male goldfinch did the foraging for the young and himself and visited the nest a little less often than once an hour. At the nest he fed the young with 7 to 10 bobs of his head and left without pause, flying down the road with three or four short, equal-valued notes, which were lower in pitch than the two-parted call that he used when approaching the nest. Between 5:05 A.M. and 11:30 A.M., the male goldfinch made four visits to the nest. These took place at 6:24, 8:04, 9:11 and 10:25 A.M. Between 3:20 P.M. and 5:45 P.M. the male made only one trip to the nest. At 8:10 A.M. on August 9, 1948, about a dozen goldfinches were spread out in twos and threes, flying a great deal; and alighting in the tops of trees. Two were chasing each other, alighting a foot apart in willow, coffeeberry, and on alder. One of them sang squeakily but persistently. It sang by itself in the top of the alder for about a minute. This behavior was continued for 5 minutes. At 8:20 about ten juveniles were feeding among rocks covered with dried algae in shadow at the edge of a low willow bush. The birds were hopping on the ground, picking things up, and alighting a foot or two up in this willow. All were close together, within an area 3 feet across. There were only six on the ground at any one time. The observer could find no concentration of food on the ground there. Possibly the birds in the flock saw one or two birds alight and the rest of the juveniles followed. In August 1951, the goldfinches commonly drank at a spring in the morning. Several females had single young following and begging from them.

On September 3 the young were still being fed. At 7:00 A.M. a female goldfinch pumped food with three to five thrusts down the gaping, extended mouths of young with quivering wings.

PLUMAGES

The green-backed goldfinch has a greenish yellow breast and belly, dull yellowish-green back, black wings with a white mark visible when perched. Head greenish with black on forehead extending onto the top of head. Beak short and stout, very similar to the junco, but darker gray. Sutton and Pettingill (1942) observed in southwestern Tamaulipas that all green-backed

goldfinches seen in March and April were molting and birds in early May were in complete breeding plumage. On April 12, 1950, a goldfinch in a willow on the Hastings Reservation matched closely the color of the flowers in the tree that was then leafing out. On July 31, 1939, the males had molted and acquired less brilliant plumage, or none was present. On August 2, 1939, both adult sexes were molting and were extremely ragged. On October 5 a male was in bright new plumage. On October 25, 1943, three goldfinches were in an arroyo willow at 7:45 A.M. One, especially, was in a bright yellow and black plumage.

WEIGHTS

A few weights recorded in western states indicate bulk of this finch, as follows. Three males from Nevada, two in May and one in June, weighed 9.2, 11.2, and 8.5 grams, respectively; a female, in August and two in September, 8.7, 10.0, and 11.4 grams.

In northern California four males collected in May weighed 8.0, 8.5, 8.7, and 10.5 grams. Two May-taken females weighed 8.2 and 10.3 grams. Two December-collected males weighed 9.6 and 9.8 grams; two females 8.4 and 9.1.

At Death Valley, in April two females weighed 9.4 and 8.7 grams; three males weighed 8.4, 8.9, and 8.3 grams.

FORAGING

Goldfinches forage in flocks through most of the year. They move through the bushes and trees that provide the major part of their food, and they sometimes concentrate on the lower herbaceous plants. Mostly, our evidence pertaining to food deals with plant materials, including buds, leaves, fruits, and seeds. Some animal food is eaten, but the kind and amount are difficult to identify by observation of the living birds.

On February 27, 1950, on the Hastings Reservation a few goldfinches were foraging on the ground beneath chamise bushes at the edge of a stand at the top of a southeast facing slope. In late afternoon on March 14, 1938, several goldfinches perched in the top of a blue oak, eating the flowers of that tree. On March 22, 1941, several goldfinches were in the blossoming valley oaks. A male, watched on the morning of March 31, fed for 20 minutes on fiddleneck. He then flew to a perch at the edge of a valley oak and 5 feet above the ground. He remained here less than a minute and flew off to a hill. About one-third of the time the bird was in this location, it was resting on woven wire netting or on low plants. Twice, it perched on the wire for about a minute. At 5:30 P.M. on April 27, 1938, several green-backed goldfinches were feeding in the new foliage in the top of a large valley oak.

By the first of June, 1941, an increase was noted among the green-backed goldfinches, but there were considerably more Lawrence goldfinches in the same places. By early July in 1939 there was a marked reduction in numbers of goldfinches in the places they frequented through the spring and summer. This seemed to result from the general drying of the plants on which they fed. At that time they spent much time drinking from the creeks. On several mornings at the end of August and the beginning of September from ten to forty goldfinches foraged on the ground on a dry pasture. Some birds perched in dead oak branches; others perched on Napa thistle and on dragon sagewort

where they fed. Other favorite perches were on telephone wires and fence wires in company with Mexican bluebirds and house finches. The goldfinches land on low bushes, such as deerweed, and they regularly forage on chamise.

Food

According to Beal (1910:73) the favorite feeding grounds of the green-backed goldfinch are in open pastures where the Napa thistle (*Centaurea melitensis*) grows. This plant is especially adapted to the wants of the goldfinch, for it throws out from the roots short stalks that bear seeds, while the rest of the plant is making growth and getting ready to produce the main crop. The goldfinches know where these seeds are, and apparently they get every one of them. Next in favor is the groundsel (*Senecio*), which grows in orchards, and on the unripe seeds of which the goldfinches feed to repletion. In the investigation of the food of this bird 476 stomachs were examined. They were taken in every month, and well distributed. Animal food amounts to 1.7 percent and vegetable food to 98.3 percent.

In Beal's study animal food was contained in 50 stomachs. The great bulk of the animal food was plant lice. These were found in the stomachs distributed through the four months from June to September, inclusive, though more than half of them were taken in August. One stomach was entirely filled with these insects, and in another 300 were counted.

He found weed seed to be the standard food of this goldfinch. It aggregated over 96 per cent of the year's diet, and in January and March nothing else was eaten. Napa thistle seed was found in 243 of the 476 stomachs. It is a small hard seed covered with an apparently "siliceous shell," with a hook at one end and a bunch of stiff bristles at the other. Generally, the bird skillfully removes this shell and swallows only the starchy pulp.

Beal made a list of seeds identified and the number of stomachs in which each species was found: Sunflower (*Helianthus* sp.) 4; Lesser tarweed (*Hemizonia fasciculata*) 1; Tarweed (*Madia sativa*) 23; Mayweed (*Anthemis cotula*) 10; Groundsel (*Senecio vulgaris*) 33; Napa thistle (*Centaurea melitensis*) 243; Black nightshade (*Solanum nigrum*) 1; Turkey mullein (*Eremocarpus setigerus*) 18; Alfilaria (*Erodium cicutarium*) 9; Black mustard (*Brassica nigra*) 1; Miner's lettuce (*Montia perfoliata*) 2; Red maids (*Calandrinia menziesii*) 1; Pigweed (*Amaranthus retroflexus*) 30; Chickweed (*Stellaria media*) 3; Catchfly (*Silene* sp.) 1; Knotweed (*Polygonum* sp.) 2; Sorrel (*Rumex* sp.) 1; Sedge (*Carex* sp.) 6.

Other foods eaten by this goldfinch in western states include: Fruit of creosote bush (*Larrea tridentata*) in Arizona and seeds attached to the long-winged carpels of cliff rose bush in New Mexico. In early March of 1910 on the Arizona side of the Colorado River, Grinnell (1914) saw the goldfinches eating the flower-heads of a composite plant (*Perityle emoryi*). In August one was eating seeds of lettuce in Alameda, California (Cohen, 1901). At San Diego in winter and spring Frank F. Gander saw goldfinches eating seeds of several kinds of eucalyptus in Balboa Park. According to Grinnell (1914) this bird is often seen feeding on dandelion heads on lawns in Berkeley, California. The same observer (1923) saw goldfinches eating on the seeds of sow thistle (*Sonchus*) on the margins of alfalfa fields in April. On December 29, 1927, about 20 green-backed goldfinches in one company were eating seeds of Napa thistle at Cone's, Tehama County, California.

Ross (1924), in a search for birds that grasp objects with the feet, saw that a green-backed goldfinch, while seeding a bachelor's-button head, bent the slight stem to a horizontal position. When through with it, the bird reached deliberately out with one foot, grasped a near-by spray, and pulled it under its feet on the original stem and ate from the new supply of seeds.

Grater (1947) observed large bands of green-backed goldfinches in late spring and early summer as they moved through the lower canyons in Utah, here and there congregating in the top of some cottonwood where the new buds were developing. According to Baird, Brewer, and Ridgway (1874:475), "Dr. Kennerly met with these birds in the month of February. He found them very abundant all along the banks of the Bill Williams Fork. They were feeding on the young buds of the cottonwood trees. At that season they were in small flocks, and the only note he heard from them was a short chirp, as they hopped from twig to twig, or flew from one tree to another."

FOODS OF THE GREEN-BACKED GOLDFINCH IDENTIFIED ON THE HASTINGS RESERVATION

Bromus mollis Linnaeus.—At 7:30 A.M. on August 3, 1939, a flock of ten goldfinches was eating seeds of soft chess.

Avena fatua Linnaeus.—At 8:15 A.M. on May 22 one was along a fence eating seeds of wild oat. In midafternoon on May 28 a male came several times to the vicinity of a gate on an old road and ate the ripening seeds of wild oat.

Avena barbata Brotero.—At 7:00 A.M. on July 27 two goldfinches near an old building were eating seeds from dried slender oat, but the plants still held a few seeds in place in the heads.

Zea mays Linnaeus.—At 5:40 P.M. on July 21, 1939, a female green-backed goldfinch at a house was clinging to the terminal panicles of maize and pecking at a central one. She did not stay more than 10 seconds. At 8:00 A.M. on August 5 one was in a garden eating at the upper, dried flowers of maize.

Salix lasiolepis Bentham.—In midmorning on April 6 one goldfinch in an arroyo willow near a water trough was eating ripening willow seeds. At 10:10 A.M. on July 28, 1942, a flock of half a dozen goldfinches was feeding on the buds of an arroyo willow. One female pried off a leaf to get the bud from the axil. Other buds were pried loose without removing the leaf. The bud scale was discarded before the bud was eaten.

Salix laevigata Bebb.—In a morning in late March two goldfinches were eating flowers of red willow. In the afternoon on April 1 ten goldfinches were in a red willow beside a creek and eating the ripening seeds. All the birds kept busy for the half-hour that the observer watched. At 9:30 A.M. on April 10 a female with a few purple finches was eating flowers of a red willow along a creek. At 8:45 A.M. on July 26, 1939, several goldfinches were eating parts of the catkins with seeds in a large red willow. These were mostly in the interior of the tree.

At 10:00 A.M. on September 15 a flock of twelve goldfinches was in a large willow. All the birds were moving about in the outer foliage, busily pecking at something on the leaves and giving various thin call notes. They all remained in one tree, some 35 feet off the ground while the observer stood watching for a 2-minute period. At the same hour a week later about ten birds worked through the upper part of a willow. Two birds clung to the outermost branches and picked at new buds. A leaf fell from the place where a goldfinch was picking.

Alnus rhombifolia Nuttall.—On January 4, 1939, a flock of fourteen goldfinches was in flight near a creek. One pair in an alder fed at cones and probably ate the nutlets. At 11:00 A.M. on January 10 a flock of fourteen in the top of an alder picked at the catkins. The birds were mixed, males and females, and some had bright plumage. On December 5 a small flock picked at cones in an alder along a creek.

Quercus agrifolia Née.—In midmorning on September 1, 1939, two immature goldfinches and an adult male clung to vertical new shoots in the top of a coast live oak, and ate the mature leaves. The birds clung beside a leaf and nibbled at its margin, usually with the side of the bill, so as to cut off a narrow strip. Then, with a twist, they pivoted around the tip of the bill, and this piece was wrenched off, eaten, and another taken. The young birds ate only five bits apiece, but the male stayed for 5 minutes and he ate intermittently on the same leaf during that time, until another juvenile flew up, alighted, and flew away followed by the male. The vertical shoots of seven out of nine trees in sight had been partly, sometimes almost entirely, denuded of leaves, probably by this feeding. As only the highest shoots were so treated, and there were not many on each tree, no great injury would ensue. Preference for green food is striking in this species. Early in the morning of September 9 one goldfinch was clinging to the end of an upright branch of live oak near the top. It twisted the head around sideways to peck at a cluster of leaves at the tip of the branch. In midafternoon some birds were feeding on live oak leaves at the tips of upper branches. On October 12 a young goldfinch perched on new growth of a live oak twig and nibbled leaves in the manner observed earlier.

Quercus lobata Née.—In the morning on January 5 four or five goldfinches near a water trough perched in the top of a valley oak and picked at terminal buds of twigs; the observer could not see clearly what they ate. A week later at the same hour five goldfinches perched at the top of a leafless valley oak. They picked at new buds on twigs at the crown of the oak. By mid-April 1948, flowers of valley oaks had attracted a few green-backed goldfinches. Two weeks later, in another year, several goldfinches in a valley oak in late afternoon were eating flowers of the tree.

Quercus douglasii Hooker and Arnott.—On March 27, 1938, just before noon two goldfinches were in blue oaks on the north side of a hill eating flowers of these trees that were then in flower and coming into leaf. In midmorning on April 6 two goldfinches were foraging in the tops of blue oaks near the edge of flats on the southeast side of a hill. They were eating the new buds.

Urtica urens Linnaeus.—On March 23, 1942, two birds were eating seeds of small nettle then ripening. The birds visited two or three plants; no insects could be found there, but numerous seeds were missing.

Phoradendron villosum Nuttall.—At 8:30 A.M. on September 4 three goldfinches in a clump of mistletoe in a blue oak were eating the berries that were just starting to grow. Two weeks later goldfinches were not as numerous here as they were at overflow water. The birds did not feed on mistletoe at once, but generally there were two to five birds standing on a sprig of mistletoe and pulling at it.

Rumex crispus Linnaeus.—At 5:45 A.M. on August 26 a flock of 50 goldfinches was feeding. Most of them were juveniles and they were eating the achenes from curly dock. At 8:40 A.M. on October 20 five goldfinches were clinging to a vertical stalk of curly dock, were pecking at it and eating the achenes.

Silene gallica Linnaeus.—At 11:21 A.M. on July 14, 1942, three goldfinches fed upon the seeds of windmill pink in the shade of a valley oak.

Lepidium nitidum Nuttall.—In the afternoon on April 5, 1938, several goldfinches in a vineyard were eating seeds of common pepper-grass then ripening.

Brassica campestris Linnaeus.—On February 8, 1939, a goldfinch perched on a flowering yellow mustard and pecked at the inflorescence, but the observer could not determine what it ate. On March 23 two goldfinches cut off two green pods of yellow mustard.

Brassica oleracea Linnaeus.—At 6:30 A.M. on July 20, 1939, one goldfinch was eating seeds on kale.

Capsella bursa-pastoris (Linnaeus) Medicus.—In the evening on April 10, 1938, three or four goldfinches were in an orchard eating ripening seeds of shepherd's purse.

Platanus racemosa Nuttall.—At 6:00 A.M. on August 7, 1942, a male green-backed goldfinch perched on the tip of a vertical twig in the top of a western sycamore. He twitched his tail vigorously, ruffled his wings, sang, and flew to a near-by slanting limb to peck at buds. A female in another tree was also foraging as if obtaining buds or insects.

Holodiscus discolor (Pursh) Maximowicz.—At 10:15 A.M. on November 20, 1939, three goldfinches in a cream bush perched at the tip of a horizontal or nearly horizontal

branch immediately above a suspended panicle. The birds reached down at foot level, or below, in order to get a billful of the achenes. Sometimes, the head was brought down three or four times in succession before it was held in a raised, stationary position for 6 to 8 seconds of munching, during which considerable chaff spilled from the edges of the bill. Apparently, only the achenes were swallowed. The bill, while held in the panicle in order to extract achenes, was opened and shut in rapid succession, as though the birds bit off pieces. One male flew 12 inches from his panicle to alight within touching distance of a feeding female. She squeaked for 2 seconds, and then flew off, allowing the male to feed on her panicle. The cream bush was in shade.

Adenostoma fasciculatum Hooker and Arnott.—At midday in early January six goldfinches fed on chamise achenes at the top of a bush. On January 16 a male and a female ate from fruiting branches of chamise. The birds were 20 feet apart at first, but the female soon flew to the male. She resumed eating about 1 foot from him. The birds perched on a stem near the dried fruits and made many successive pecks into the panicle. They obtained great quantities of food in this manner. After 5 minutes the pair flew away over the chamisal. On a morning in January twelve goldfinches fed on chamise achenes at tops of bushes. No calls were uttered. The next morning fifteen goldfinches clung to tops of bushes halfway up a slope. All were busily eating achenes, and they uttered only occasional calls.

In early February one male fed at chamise panicles at 10:20 A.M. In mid-February a pair fed on achenes. At 9:30 A.M. on February 15 a flock foraged in chamise on an east-facing slope. The entire flock was feeding within a radius of 15 feet and in one place seven birds were feeding within a square yard. They ate achenes from the slender reddish upright panicles. They fed from a variety of positions, but usually by clinging to the leafy part of the stem and reaching upward for the fruits. They seemed to swallow the achenes whole. The *did-did* call was continually heard. In early afternoon most of a flock of fifty birds of this genus fed on chamise in a pasture. These birds fed rapidly—ten or more to a bush—and they stayed for several minutes. In the pasture they harvested the achenes for so long that an appreciable reduction had taken place. More than half the achenes had been removed by birds. The observer was unable to see peculiarities in manner of feeding that would distinguish any of the species or either sex. The flocks were mixed and the behavior almost identical.

For nearly 3 hours in the morning on February 16, 1939, a widely scattered flock of ten birds foraged in chamise. They were separated so far apart that the observer could not see more than two at a time. He could, however, hear them calling from different parts of the slope. They spent some time in the blue oak and live oak trees in the bottom of a ravine where they flew singly and called. They perched for a minute or so on the terminal twigs, and they usually foraged by reaching for the fruits both above and below the perch. In midmorning on February 17, 1938, six Lawrence goldfinches, one pine siskin, and one green-backed goldfinch fed as a flock in chamisal. After 4 minutes the Lawrence goldfinches flew leaving the pine siskin and the green-backed goldfinch feeding together. The birds gathered the achenes. Often they fed not more than 3 inches apart on the same branch. They seemed equally active and the observer could detect no difference in the method of feeding. Often they had to reach up for achenes, occasionally one hung upside down. In the morning during a light rain in February a male and female within 4 feet of each other ate achenes 250 feet within the chamisal on a ridge. When aware of the observer's presence they instantly dropped out of sight into the chamisal.

In the morning in late June a female fed among flowers of chamise. A male joined the female and both birds perched and worked at clusters for 5 minutes. The flower clusters showed the brown of withered flower parts; possibly, the ovules were eaten, as in fiddle-neck. On July 1 several goldfinches in the chamise ate ripening fruits. Four days later one ate new achenes. On July 25, 1948, an adult male green-backed goldfinch fed in company with Lawrence goldfinches in chamisal. In contrast to the Lawrence goldfinches, it perched on flowering branches in middle height in these bushes, 3 feet up or less, and leaned far forward and down or hung upside down in efforts to reach all parts of the flowering branchlets. It took the drier fruits as did the Lawrence goldfinch. It uttered no calls until five birds were startled into flight by a flicker; then in flight it made slight jarring notes. Later an adult and an immature returned to feed.

In early August an adult female ate achenes. She ate ten achenes from one panicle, evidently one at a time, then flew 10 feet to another cluster. There was no alarm or ob-

vious reason for changing, or for choosing any particular one. The bird perched at the base of a cluster. From the middle it ate 20 or 30 achenes. The feeding time was $\frac{1}{2}$ minute at the first place, and 1 minute at the second. At 6:20 A.M. a female fed on chamise again. At 11:00 A.M. on August 9 three goldfinches ate achenes in sunshine. They prefer to eat in sunshine rather than in shade, but they rest in live oaks, and make sorties out to forage from time to time. At 9:00 A.M. on August 19 a flock of seven goldfinches flew from willows along a creek 50 yards into chamisal where they removed flower receptacles from the spikes.

At 8:20 A.M. on September 4 a flock of fifty green-backed goldfinches assembled at the margin of chaparral on a hill. A few foraged in tops of two live oaks, but most of them ravenously devoured achenes of chamise; only a second was required for a bird to snatch an achene, roll it with the tongue between the champing mandibles, discard the husks, and swallow the fruit. At 10:00 A.M. on September 8 a small flock of green-backed goldfinches with Lawrence goldfinches ate achenes of chamise.

In afternoon on November 11 on a small hill, a flock of sixteen goldfinches fed on chamise. The birds perched near together on the outer dry, brown panicles. They fed rapidly; one pecked seventeen times in 20 seconds, and apparently it obtained an achene each time. Later in the month numerous green-backed goldfinches in blue oaks and in chamise ate achenes. At 4:15 P.M. near the end of November about six in a flock with other *Spinus* ate achenes from bushes at the edge of a patch. Each bird perched directly on a panicle and picked off the achenes. In midmorning one perched on chamise and pecked at the brown panicles of achenes. As the bird pecked only at the achenes and as each mouthful was munched, the chaff spilled from the edges of the bill.

Erodium cicutarium (Linnaeus) L'Heritiere de Brutelle.—At 8:00 A.M. on June 28, 1938, a female goldfinch perched on a stem of buckwheat and picked off ripening seeds of red-stem filaree.

Eremocarpus setigerus (Hooker) Bentham.—In midafternoon on November 19, 1944, some goldfinches stood on tops of turkey mullein plants and ate the seeds.

Aesculus californica (Spach) Nuttall.—At 8:30 A.M. on July 1, 1938, several goldfinches were present in a canyon. A young bird in the top of a buckeye perched next to a flower cluster and picked at flowers half a dozen times before it flew away. The observer could not see what it got, but the vigor with which it pulled seemed to indicate that it was taking a part of the plant.

Ceanothus ramulosus (Greene) McMinn.—While a flock of goldfinches waited to go to water, just after arriving at a small stream in midmorning at the end of July, the birds sometimes ate leaves of coast ceanothus. These were worked with the bill as the bird perched on the stem and cut off and worked small bits in the bill before swallowing them. Not much was eaten at one time by the birds, indicating that the leaves were not very palatable. A young bird nibbled at the margin of a leaf, already somewhat ragged. Bits of margin $1/16$ inch in diameter were cut off, chewed up in the bill, and swallowed. Just before the bird ate this, it opened the bill and snapped the tongue against the roof of the mouth (no sound was audible at 20 feet). Whenever the young one began to nibble a leaf-edge, the female drove it away and nibbled there herself. Two young begged for food, but were not fed. The female chased one away when it begged. The young bird and the female tried to feed from empty capsules but they were unable to obtain food: the tip of the bill was used, pinching inside the cup. The female nibbled at the outside of a dried capsule still on the plant, but the observer saw no food removed. There was no attempt to take a seed out of the capsule.

At 8:25 A.M. on August 2, 1939, three birds rested and preened in a ceanothus beside the running overflow of a water tank. One was resting and preening. One cut off margins of leaves of ceanothus and ate them. At 11:15 A.M. six birds ate the leaves. Feeding on leaf-margins of ceanothus was more common than had been observed before: at least one bird ate leaves most of the time in the area in view. The next day at 4:40 P.M. five birds, 1 adult and 4 juveniles, perched in sunlit ceanothus. The young ones ate leaves, while a male adult merely sat in the sun and preened occasionally. Two young were clinging to vertical stems, eating terminal leaves, and most of the leaves near the tips were cut or gone, as if goldfinches had fed there. The other two perched on horizontal stems and cut off margins of leaves before them. At 9:30 A.M. on August 9 a male and a female fed on terminal leaves of ceanothus. This was not frequent in this ravine, although bushes were

plentiful. The next day at 10:00 A.M. three goldfinches ate leaves of this plant. When they went to water, the adult drove away a young bird by once pecking at it; then the adult bathed in its place. A week later between 5:00 and 5:45 P.M. several birds in ceanothus near a water tank overflow, ate leaves.

On September 1 in the bushes where the green-backed goldfinches spent much time in August, certain stems in the tops of plants had been denuded except for the terminal bud. This undoubtedly resulted from the feeding of these birds, but again only a few stems were so treated, and no injury had occurred to the plants. One ate mature leaves. Although several other birds were in the bushes, they showed no inclination to eat the leaves. At 8:53 A.M. on September 9, 1939, 15 yards below a water tank, four goldfinches fed on coast ceanothus leaves. They preferred small leaves close to the tip of a branch, for the bird has to pull hard to break off part of a leaf. At 4:45 P.M. in mid-September six goldfinches in a ceanothus bush beside a water tank overflow ate buds along the slender stems. At 3:25 P.M. on December 9, 1939, two perched on ceanothus, bit off, and swallowed pieces of the leaves. Full-sized leaves were eaten as well as those at the tips of the branches.

Rhamnus californica Eschscholtz.—In the morning on August 31 three or four goldfinches with house finches ate fruit in a coffeeberry beside a creek. The birds picked at the pulp of ripening fruit and left the remainder attached. Apparently they sought only the juice. At midmorning on September 14 two goldfinches on tips of upper branches of coffeeberry bushes pecked at ripe berries. On September 22 one ate fruit in a coffeeberry thicket by pecking into pulp and leaving the berry attached. In early afternoon the next day six green-backed goldfinches ate coffeeberries by pecking into the still attached fruit; the birds seemed to have some difficulty getting at the berries. Two days later one pecked at a berry. At 3:30 P.M. on October 17 one goldfinch nibbled at two ripe fruits, but ate very little of either.

Rhamnus crocea Nuttall.—About 8:30 A.M. on August 11 half a dozen goldfinches lit in a bush of redberry. They ate the fruit by picking off pieces from the side. They did not pull off the whole berries. About 11:00 A.M. three fed on redberries in another bush. A week later a small group of goldfinches around a redberry bush on a hillside ate the fruit by pinching out the juice. In midmorning on August 22 one goldfinch accompanied house finches in a redberry bush. The goldfinch moved to redberries from which pulp had been taken by a lazuli bunting and picked at the remaining nutlets. This habit of picking up leavings may account partly for the habit of following other, larger species in flight and in foraging. In the morning on August 28 one goldfinch with Mexican bluebirds ate fruit of redberry.

Around 10:00 A.M. on September 1 one of two goldfinches in a canyon lit in a redberry bush and began to eat ripe fruit by picking pulp. At 4:15 P.M. toward the end of the month three goldfinches ate redberries on a 6-foot bush. Each bird perched near a berry, leaned over, and picked at it, thereby getting a small amount of the fruit. The bird would straighten up, nibble for 2 seconds, swallow, lean over, and pick a little more from the berry. This was repeated six times at one berry before moving to another perch and repeating the procedure. All the birds fed at the top of the bush. Four berries were nibbled by each bird in a 45-second period. Twenty goldfinches chattered from their perches at the top of a near-by 15-foot valley oak at the same time the three birds ate redberries. In late afternoon on October 16 one ate fruits.

Datisca glomerata (Presl) Baillon.—From 5:10 to 5:15 P.M. on August 8, 1948, a pair fed silently two-thirds of the way up the stems of durango root, dead and dried up, at the side of a creek. There were no other goldfinches near, but some could be heard in the distance. These birds fed first on separate stems 18 inches apart, then together on the same vertical stem, the male 6 inches above the female. They ate slowly, every 5 to 10 seconds leaning forward or upward, picking at the vegetation, then working something in the bill with rapid, slight movement of the mandibles. An examination of the stem revealed no opened capsules, but they were so dry they broke off entire. The observer could not see which part of the plant the birds ate. If they had been taking seeds, the capsules would have been plucked off and because they are large, they should have been seen. The food must have been the seeds, for there were no insects on the stem; the seeds are small and it would take close watch to determine how the birds get them.

Clarkia elegans Douglas.—At 8:00 A.M. on August 1, 1942, a female fed on seeds

of canyon clarkia, carefully removing part of the capsule before swallowing the seeds. She was particularly nervous at the beginning of feeding. She pumped her tail, twitched her wings, and then became more steady. She ate about 10 seeds and flew.

Epilobium franciscanum Barbe.—On February 8, 1939, three goldfinches fed on a coast cottonweed. They frequently lit on the slender branches, which bent down with the bird's weight; then they worked, head down, on the seed capsules. They seemed to get only one seed with each downward stroke of the head.

Godetia quadrivulnera (Douglas) Spach.—On October 29, 1938, several goldfinches at a roadside ate seeds of four spot.

Conium maculatum Linnaeus.—At 8:10 A.M. on July 19 an observer saw a pair of goldfinches feeding on the seeds of poison hemlock, growing in a mass of poison oak. In the morning of July 20 two males beside a creek ate seeds of this plant and, possibly, aphids.

Late in the morning on July 27 five goldfinches fed on ripening seeds of poison hemlock. There were no flowers; most of the seeds were still green, and some receptacles empty because seeds had fallen out or had been eaten by birds. At mid-morning on August 10 a dozen goldfinches were foraging on poison hemlock; apparently they ate both leaves and seeds. At 10:00 A.M. on August 16 a female and a juvenile fed on poison hemlock.

Arbutus menziesii Pursh.—On August 20, for 15 minutes half a dozen goldfinches, in the top of a madroño tree on a slope above a creek, picked at fruits and ate them. On August 22 a group of at least eight goldfinches foraged in the top of a madroño tree beside a creek. They picked up the berries of the madroño. One clung to a panicle and picked at the base of the fruit. This group remained in the tree more than 10 minutes. Near noon on November 20, two goldfinches pecked persistently at ripe fruits of madroño, apparently picking off and eating minute pieces.

Eriodictyon tomentosum Bentham.—In the morning on August 2 a goldfinch perched at the base of clusters and ate green seeds of woolly yerba santa. The bird wrested out seeds one at a time, worked them in its bill, and swallowed them while it remained perched on the plant. As usual, a flip of the bill threw aside seeds sticking to the outside, tossing them 2 or 3 inches. An hour later another bird ate the sticky seeds. At 10:30 A.M. on August 10 three goldfinches perched on a stem and ate a cluster of ripe seeds. Some effort was clearly required to get the seeds out of the plant, and after being removed, the birds moved them about in the bill for 10 seconds to crush them before they were swallowed. One bird ate four seeds; the other two ate three each. No seeds were scattered or carried away. Goldfinches were still numerous in the vicinity. On the morning of September 9 one bird fed on the seed head of woolly yerba santa 4 feet from the ground. It perched on a raceme. The bird pecked once; then holding up its head, it opened and closed the bill.

Plagiobothrys nothofulvus (Gray) Gray.—At 8:00 A.M. on April 2 a flock of twenty goldfinches on a slope perched on stalks and ate immature nutlets of rusty plagiobothrys. On April 10 a flock foraged over a slope and fed almost entirely on the nutlets of rusty plagiobothrys which that year grew in a remarkably thick stand. At 8:15 A.M. on April 25 about twenty goldfinches fed on the maturing nutlets of rusty plagiobothrys on a knoll.

Amsinckia intermedia Fischer and Meyer.—From mid-March to mid-June these goldfinches spend a great deal of time in the patches of common fiddleneck in open areas that were formerly cultivated. The birds eat the nutlets while they are still green. Ordinarily the plants reach a height close to 30 inches and they grow in dense stands. This food is available in abundance through the nesting season and even after the young are fledged. The birds sometimes search for the dried nutlets on the dead plants as late as November and December.

Sometimes single birds fed in the patches of fiddleneck and sometimes they came in flocks. Single birds are likely to be feeding early in the season.

In early afternoon on March 14 a goldfinch foraged about 1 minute in fiddleneck. In early morning on March 31 a male fed 20 minutes on fiddleneck.

In early afternoon on April 6 a small group of goldfinches ate aphids in an apple tree and on adjacent tall fiddleneck. At 8:00 A.M. on April 6 a pair was in an orchard eating green nutlets of fiddleneck. At 8:30 A.M. on April 11, in a fog, several green-backed goldfinches along with Lawrence goldfinches were picking out and eating nutlets of fiddle-neck. At noon on April 14 half a dozen goldfinches were in an orchard close to a house

eating nutlets of fiddleneck. In the morning of April 24 a pair was eating fiddleneck. In mid-April, 1948, the ripening of fiddleneck attracted a few green-backed goldfinches, the first seen in several months.

In midmorning of May 1 a goldfinch on a stalk of fiddleneck pecked at the seed heads, apparently eating the green nutlets. On May 23 two pairs fed together at a roadside. At the end of the month a feeding flock contained twenty-five birds. In other years increased numbers came to the patches of ripening fiddleneck in the last week of May. In June there were young birds as well as adults in the fiddleneck patches and Lawrence goldfinches were also prominent there. Males tended to be prominent in the flocks. Increased numbers in the last week of May, 1950, brought birds that fed on the ripening fiddleneck that was especially abundant that year.

Early on June 14 two green-backed goldfinches and one Lawrence alighted on a fence. They flew together to a patch of fiddleneck and fed on the ripened nutlets. Another Lawrence goldfinch joined them. All the birds appeared to be adult males. They fed in harmony, 6 inches to 3 feet apart. In the morning on June 17 goldfinches were eating nutlets of fiddleneck.

Near noon on November 1 the air was sunny and warm 45 minutes after a 5-hour light rain; three goldfinches fed for 7 minutes among the dead stems of fiddleneck. When the observer walked to the exact spot where one had been feeding, he found nutlets occasionally in the dried heads of the plant, but he could not see exactly what the bird had eaten. The rain had ruptured the capsules and made the nutlets more easily available.

At 8:20 A.M. on December 7 a flock of 21 goldfinches fed on the dry, dead stalks of fiddleneck, searching for nutlets. They gradually moved up the field. They remained in the sunlight, avoiding areas still heavy with frost in the shade of the willows. When a flock of white-crowned and golden-crowned sparrows suddenly flew up 60 feet to a blue oak from bare ground and 80 feet from the finches, about half of them flew 100 feet to some willows, the nearest cover. They began returning after 10 to 15 minutes. After 20 minutes they had moved up 120 feet and were feeding in an area of frosty plants and in the partial shade of a leafless valley oak. Another alarm drove them to the closest willows and coffeeberries.

Verbena lasiostachys Link.—On October 3, 1939, a goldfinch at a fence near a creek fed on the nutlets of common vervain. It perched on the stem, bending it horizontally. The bird then reached to the fruits. It stretched the neck and reached inside the calyx to extract dry nutlets.

Trichostema lanceolatum Bentham.—Late in the afternoon in early September a group of seven goldfinches fed on vinegarweed. They flew up to 15 to 20 feet in black locusts 40 feet away when the observer passed by. Before noon in late September two goldfinches perched on bare stalks and fed on nutlets of vinegarweed. At 8:00 A.M. on September 20, about 35 birds fed on the ground in a stand of vinegarweed. On September 30 at 7:20 A.M. a flock of 12 to 15 goldfinches which had fed daily on fruits of vinegarweed after they began to ripen about the tenth fed on the fruits in a patch.

At 8:35 A.M. on October 4 sixteen goldfinches fed on maturing fruits of vinegarweed in a corral. The birds were in the thickest growth of plants 10 to 18 inches tall, and they fed 6 inches to 3 feet apart. In perching on a stalk to feed, the birds clung with feet 1 to 1½ inches apart, and from the stalk above their feet they picked nutlets, exposed in open cups. The abundance of fruits and leisurely manner of feeding did not require frequent moving. Birds moved up the stalk, never down, but they usually did not feed over more than 4 or 5 inches of any stalk. One bird fed at the fruits where it first clutched the stalk; then it worked up without moving the feet. By October 19 this species continued to feed on the abundant supply of vinegarweed fruits maturing at a barn lot. A flock of 13 were so engaged. At 2:05 P.M. on October 19, six birds clung to the vertical spikes of a single vinegarweed and pecked at the plant about the flowers and fruits. The part of a spike where the bird pecked had many capsules containing ripe nutlets. When the disturbed birds flew to a wire fence, they returned within 1 minute, after the observer moved 15 feet away. Some pecked at a spike with slightly open bills, raising the head after each peck, and each one munched three to five times, but no chaff fell. The structure of the open capsule enables the bird's bill to fit into it and extract the nutlets without any foreign matter. On a knoll sixty goldfinches in a compact group fed on vinegarweed. Some perched near the end of the flower spikes and thereby caused the spikes to bend to a horizontal position; they pecked at the seed capsules clustered about their feet. Others clung to a

spike which remained vertical, and pecked at seed capsules either above or below. Still others clung to dry oat stalks to peck at the adjacent vinegarweed spikes. An hour later thirty birds clung to the vinegarweeds between a creek and a road. The bill was inserted into the open capsule to extract nutlets; the head then was raised for 1 or 2 seconds before another peck. On October 23 sixty goldfinches on a knoll fed on vinegarweed. At noon on October 25 six goldfinches extracted and ate the nutlets on a vinegarweed. For the last 4 days of one October the customary hordes of green-backed goldfinches were not present on the fields. Examination of the vinegarweed plants on a knoll revealed no fruits in any of the capsules. However, many of the plants had green, unopened capsules. Hence, return of the goldfinches was expected.

At noon in early November two birds clung to vinegarweed to eat the fruits. The observer could see no other goldfinches. Early on a November morning four goldfinches fed on green fruits of vinegarweed in a sunlit field. They clung to semi-vertical stems, which did not readily bend beneath their weight. There was only one bird to a stem. The birds sometimes ate head downward, but the vertical position with head up was most often used. They ate from the same stem they used for a perch. Small groups all over this field foraged principally on vinegarweed. Sometimes one foraged on the ground, but not for long. In midafternoon on November 6 one male goldfinch flew to a stalk of dead vinegarweed. Hanging from near the top he leaned down and picked out tiny objects from the dry receptacles. The plant had many dry fruits. Late in the morning on November 8 four goldfinches fed at the stalks of vinegarweed near a spring, extracting and eating fruits. Other birds came later to water at the spring. In the late afternoon on November 9 a goldfinch ate vinegarweed fruits in a stubble field. The bird perched at the top of a plant 15 inches high, and it was joined shortly by two other green-backed goldfinches which perched on the same plant and ate seeds also. At 10:30 A.M. on November 10 a male was near a flock of Mexican bluebirds by a fence on top of a hill, eating fruits from an upright plant of vinegarweed. The plant had empty capsules where the bird had pecked, as well as ones full of nutlets elsewhere on the stem. Also there were numerous blossoms. At 10:40 A.M. on November 11 on a knoll one bird stood on the ground and fed from the capsule of an adjacent vinegarweed. Another bird was within 4 inches of the ground. An hour later a flock of eleven fed on stalks of vinegarweed. The plant chosen was greener than the others immediately around it. Early in the afternoon on November 18 both males and females clung to 1-foot stalks of vinegarweed, picked at the dry capsules, and ate the nutlets.

On December 1 after showers the previous night continued until 8:00 A.M., a flock of about fifteen birds flew from a patch of vinegarweed to willows 75 feet away. They alighted 3 to 10 feet aboveground in the 25-foot thicket. At 11:05 A.M. a flock of about 30 flew 25 feet to a willow from a 15-foot long patch of vinegarweed. In mid-January four males and two females perched on vinegarweed and pecked at the open capsules.

During a moderate fall of wet snow on February 6, 1948, when the ground was lightly covered, a flock of 14 goldfinches fed on drooping and sparse stems of vinegarweed in the middle of a field. They foraged in the same manner as in sunlight; however, because of the low stems, they often alighted on the ground, picking at fallen nutlets, or at low, nearly horizontal stems. Occasional *chip* and *see-se* notes were sounded. The snow, then, is not a detriment to feeding green-backed goldfinches if it is not so deep that it covers the vegetation.

Marrubium vulgare Linnaeus.—On July 26 five goldfinches, at one time in a small cluster of horehound, shelled and ate nutlets, 10 feet from a water trough where they had been drinking and bathing. On August 3 a flock of ten birds ate nutlets of horehound. In early morning on August 17 fifteen goldfinches fed on a hillside. Some ate nutlets of horehound from heads still showing some green, although adjacent heads were fully ripe and brown. The next morning twenty-five goldfinches in a compact flock ate nutlets of the horehound. On August 6 two birds near a water trough ate nutlets of horehound. In early afternoon on October 19 one bird clung to a horehound stalk and pecked at nutlets.

Salvia columbariae Bentham.—Contrast in kind of food taken by green-backed and Lawrence goldfinches in a mixed flock showed a persistence on the part of each species to limit its feeding to a single kind of seed. The impression was strong that each kind of goldfinch had a firmly established tradition in selecting the food it ate.

At 3:30 P.M. on May 4, 1940, six birds perched at the edge of burned chamisal at

the base of a hill. One clung to an oat stalk and pecked at a chia head. At 10:30 A.M. on May 20, 1938, a flock of twelve, or more, on the lower part of a burned area, perched in burned chamise branches and ate the ripening nutlets of chia from the heads.

On July 1, 1938, three or more green-backed goldfinches with a small flock of Lawrence goldfinches foraged among sandy washes between the base of a hill and a creek. They ate nutlets picked from heads of chia, even though the other species of goldfinch, often only a few inches away, for the whole time picked nutlets of *Cryptantha muricata*.

Salvia mellifera Greene.—The earliest use of black sage by this goldfinch was recorded late in the morning on June 4, 1940, when a pair ate ripening fruits. On July 2, 1939, several green-backed goldfinches foraged on a chamise-covered slope. For more than 5 minutes one male shelled and ate nutlets from ripening whorls of black sage near the bottom of a ravine. The bird was frightened away, but he returned a minute later in company of another male and resumed feeding. This period lasted for another 5 minutes during which he visited 10 whorls and extracted several nutlets from each. He removed and discarded the papery covering of each seed. The heads were still greenish—not yet hard. In the morning on July 12 two goldfinches fed on ripening seeds of black sage in the bed of a creek. Each bird picked out nutlets rapidly and worked each one through the bill, possibly to remove the covering before it was swallowed. It stayed in the same small bush, but moved from stem to stem frequently, constantly picking at new whorls. Finally, a slight movement 20 feet away frightened the birds. At 9:05 A.M. on July 17, 1942, two birds foraged on black sage near a creek. Probably ten birds were in sight and sound. On July 19, 1953, a male and female green-backed goldfinch fed on black sage for 2 hours from 9:30 to 11:30 A.M. These two birds remained less than 3 feet apart as they foraged. They had been there the previous day also. At 6:00 A.M. on August 6, 1942, three males and one female on a wire fence fed on black sage.

Nicotiana bigelovii (Torrey) Watson.—Once on a July morning a green-backed goldfinch lit on a stalk of Indian tobacco and picked for a few moments at a capsule. On November 7, 1937, two goldfinches fed on small dry seeds of this plant on a stalk at the side of a road.

Cordylanthus rigidus (Bentham) Jepson.—At 8:00 A.M. on August 3, a flock of goldfinches was eating flowers or green seeds of bird's beak beside a road. At 5:00 P.M. on August 8, in shadow, several goldfinches on the side of a canyon clung to green plants of bird's-beak and ate at the flowering heads or seeds. At 5:45 A.M. on August 16, 1942, a flock of 50 birds, most of them juveniles, ate seeds of bird's-beak. Three days later twelve birds ate green seeds of bird's-beak in the morning. In late afternoon on September 2 several goldfinches were in blue oaks. Three birds lit in flowering plants of bird's-beak and ate the flowers or parts of them, but they were frightened away. Early in an afternoon in mid-November several birds ate seeds of bird's-beak.

Sambucus coerulea Rafinesque.—From 7:30 to 8:00 A.M. on July 22 several goldfinches in an elderberry bush ate green drupes. Later in the month two birds in an elderberry bush ate drupes. In midmorning on July 27 beside a creek, a female fed on drupes of blue elderberry. At 9:45 A.M. on August 15 two birds ate drupes in a blue elderberry bush along the creek. They perched repeatedly in the same bush. A week later one ate drupes in an elderberry bush beside a creek.

Lonicera interrupta Bentham.—On May 21, 1939, a male ate buds and flowers of chaparral honeysuckle. In early morning on August 3 birds in a flock beside a road ate flowers. A week later on the side of a hill about 8:15 A.M. one ate green fruit. On August 20 six birds fed on the dried flowers. A bird would perch on a horizontal stem beside a flower or swing downward beneath flowers on nearly vertical stems and peck at a head. The ripening ovules were probably being eaten. At 9:15 A.M. on August 22, 1939, one ate green fruits.

Madia gracilis (Smith) Keck.—In midmorning on June 1, 1939, a pair of goldfinches tore apart receptacles of gumweed. The birds worked only on the lower receptacles which contained mature achenes. The plants had the yellow rays just showing on some upper receptacles. In afternoon on June 9 a female fed on gumweed. She perched on a bent oat-stem and reached out 3 inches to achenes in cups of receptacles. Sometimes achenes came out easily and sometimes with difficulty. Achenes are in spoon-shaped bracts, and are scraped out one at a time with the tip of the mandible, as the bill is drawn away from the plant. The containing bracts remained on the plant. Sometimes the female pulled harder

and the receptacle also came off. These stuck to the bill because of the sticky secretion on the plant, and they were shaken off with several lateral jerks of the head. Achenes were also thrown off in this manner; the sticky substance made it difficult to remove them, but the bill was not scraped, nor was a foot used. One achene fell 8 inches from a plant and another fell 6 inches in another direction. By these forces, achenes would probably not be distributed farther than 3 inches from the plant. On the plant there were four heads: three ripe and one unripe one had flowers. The ripe heads were eaten but not the unripe one. Four achenes out of thirty mature ones were left. The female called *whit-whit* when the stem collapsed under her. This may be a surprise note or a warning note.

At 11:40 A.M. on July 21 1941, a male goldfinch perched for about 30 seconds on a wire and then flew to a gumweed where he ate the achenes. He was about 30 inches from the ground where he pecked at a head and cracked the achenes in his bill. A female flew, 15 seconds later, to the same kind of plant 2 feet from the male. She flew to the top of the 18-inch plant. The plant bent under her weight, and then she started to eat the achenes in the same fashion as the male. After taking an achene in her mouth, she shook her head. This procedure enabled her to get rid of the achene coat after she had cracked it open. The birds fed for 2½ minutes and then the male flew into dense growth; the female followed him immediately.

Lagophylla ramosissima Nuttall.—On July 7, 1939, two goldfinches perched on the upper branches of slender rabbit-leaf and ate the flowers or the developing achenes. No mature heads were found. In the morning on August 12, 1948, a flock of fifteen goldfinches ate seeds of slender rabbit-leaf which grew tall and was still in flower.

Helenium puberulum De Candolle.—Early in the morning on August 19, 1942, goldfinches fed on both yellow and brown heads of rosilla; each bird ate about ¼ of a head with a dozen strokes of the bill.

Achyranthes mollis Schauer.—In mid-May a flock in a clearing on a hill ate achenes of blow-wives. A week later six goldfinches near the summit of a hill fed on a patch of blow-wives. A bird would approach the stem on a slant, alight, and bend it to a new, horizontal position. It pecked at outer bracts, and removed some to expose ripening achenes. It would hull out an achene, strip off pappus, swallow the achene, and obtain another. On May 31, 1942, goldfinches were numerous and active among blue oaks on top of a hill. Some fed on low plants, probably blow-wives, which were abundant there, and many of the achenes were already missing.

Artemisia dracunculoides Pursh.—At 7:30 A.M. on September 2, 1950, a flock of goldfinches on dragon sagewort ate the fruits.

Artemisia douglasiana Besser.—In midmorning on July 12, 1939, one goldfinch picked at heads on a last year's stem of California mugwort. Early on August 16, 1949, an adult male tore three flower heads from California mugwort and ate them by leaning out toward the plant from a willow twig 1½ inches away. The broken pedicels were left on the panicle. Previously, at the same place two goldfinches had followed the same procedure in foraging. In the morning on August 18, 1942, a female and some juveniles ate the green flower heads. Some birds perched on stems, others perched on adjacent willow twigs and reached for the swaying heads. In midmorning of October 6, 1942, one ate California mugwort flower heads.

Cirsium coulteri Harvey and Gray.—On August 15, 1939, a flock ate achenes from western thistle. Early in the morning on August 16, 1942, a flock of fifty goldfinches fed on the achenes of this plant. Most of them were juveniles. On September 11, 1939, three goldfinches fed on western thistle by perching at the edge of a head and pecking at achenes in the center. In early afternoon on September 23, 1938, several goldfinches on heads of western thistle ate the achenes, after first pulling out and discarding the pappus bristles. On October 21, 1938, one bird at the edge of a field lit on a stalk and reached out as if to eat achenes from a head, but then it flew away.

Centaurea melitensis Linnaeus.—On the Reservation Napa thistle is one of the most prominent food plants for green-backed goldfinches from early June through September. Two records show that the achenes are also eaten sometimes in February. On February 2, 1939, at 11:30 A.M. three females ate Napa thistle. They perched on stalks and reached out to neighboring heads, picked off achenes from the plant, and swallowed them. On February 7, 1946, at 4:04 P.M. a goldfinch fed on achenes which it plucked from the

heads. The bird perched on the vertical stalk about $\frac{1}{8}$ inch in diameter and a little more than a foot aboveground. The bird then flew to another near-by stalk for more achenes. Sometimes when the stalk was weak, it bent to the ground, but the bird stayed on it until the food was exhausted. In midmorning on June 1, 1939, a pair of goldfinches was tearing apart the heads. They worked only on the lower ones. The plants had yellow flowers barely showing, one or two per plant. In the evening on June 13, 1948, a male fed at a stalk. After 20 seconds the bird was frightened away. The goldfinch had pecked away $\frac{1}{4}$ of a ripening achene on the green plant, searching for the achenes. On June 17, 1941, in the morning, goldfinches ate achenes of Napa thistle.

In afternoon on June 21, 1938, six birds picked at a head of Napa thistle with mature achenes. They pulled hard but the observer did not see what they took. Late in the morning of June 23 a male ate achenes. On June 24, 1940, a lone male ate achenes. Most of the day on July 3, 1939, thirty goldfinches ate ripening achenes. There were usually some (5 or 6) of these birds in the field eating achenes. Near noon on July 5, 1939, a female green-backed goldfinch accompanied by a wing-quivering juvenile was with a small group of Lawrence goldfinches. This bird picked out and ate achenes. The young one finally began to pick at the heads of the same plant. The other species fed, but only on the nutlets of fiddleneck. Later, farther up the field, many more green-backed goldfinches kept strictly to the Napa thistle, although it was scattered among other plants. In midmorning on July 9, 1938, an adult male took 10 minutes to pick out the achenes of a flower head and eat them. He seemed to eat the pappus also, not just the achenes.

In early August 1939, a flock beside a road ate dried achenes. Later a flock ate achenes and some birds picked at dried heads. In midmorning on August 12, 1942, a dozen goldfinches fed on Napa thistle in the shade of oaks along a creek.

At 7:30 A.M. on September 2, 1950, a flock of about ten goldfinches pecked at Napa thistle heads. At 8:20 A.M. on September 7, 1947, seven goldfinches fed on exceedingly dry and dead achene capsules. In early afternoon on September 23, 1938, goldfinches ate achenes.

Centaurea cyanus Linnaeus.—On July 2, 1949, and on several days in the preceding month these birds ate the ripe achenes of the bachelor's-button about a house. Both adults and young, mostly one or two at time, came to feed here.

Sonchus asper (Linnaeus) Hill.—On May 21, 1940, one goldfinch ate achenes of prickly sow-thistle. At noon on July 9, 1939, one perched on stems of this plant, picked off and ate plant lice found there.

SALT FEEDING

Peterson (1942) has studied the salt feeding habits of the green-backed goldfinch. Salt was offered continuously in a partly wooded pasture at 900 feet elevation on the side of Mount Diablo, Contra Costa County, California. A near-by watering trough attracted seventy species during the year, of which four were seen to eat salt. Goldfinches picked at crystals occasionally, but most of their feeding was from the earth within a foot of the block. These birds came in flocks and covered the salt-saturated ground. Eventually the blocks would be supported only by a tiny pedestal of dry earth, partly because of the salt dissolving at points of contact and partly because the birds ate soil and salt from underneath. With the passing of winter the goldfinches became less numerous.

In the morning on June 6, 1939, an observer on the Reservation saw a male goldfinch pecking at the ground near an old salt block. The man tasted the ground and found it salty. At 9:00 A.M. on July 11, 1938, a goldfinch with a house finch was at an old salt box on the ground picking up something on the bare earth. At mid-morning on November 2, 1948, two goldfinches flew up from a salt lick and into a blue oak 20 feet away. In midmorning in early November four goldfinches went to a salt block near a water trough and started directly to eat as they perched on the salt.

EATING SAND

Baird, Brewer, and Ridgway (1874:475) reported that "Dr. Heermann states that he found these Finches abundant in the northern mining regions of California, frequenting and feeding in the same localities with the *C. lawrencii* and often associated with the Pine Finch. He adds that, while thus associated, he shot a large number of both species. They seemed to be employed, at the time, in picking out the fine gravel mixed in the mud used as mortar for a chimney, flying away at each discharge of the gun, but returning, in a few minutes, to the same place."

On the Reservation at 2:00 P.M. on July 12, 1938, a pair of goldfinches moved from a willow down to the soil in a road. The male led and the female followed closely behind. They picked at several grains of sand and flew away.

USE OF WATER

Goldfinches live on dry land where the food supplies are mainly buds and developing fruits. The birds apparently need large amounts of water to combine with the seeds they eat. In the dry seasons these birds concentrate about supplies of water in streams and springs. They also go to houses where they can find dripping faucets and pipes. Availability of water is important in the nesting season and afterward when the water becomes scarce. The distribution of water helps to determine where the goldfinches live.

Woods (1925) has written about his observations on a curious psychological difference between the green-backed and Lawrence goldfinches, which are nearly identical in habits and often flock together while feeding. The difference is seen when a choice of water sources is offered. His observation was that the green-backed goldfinch always prefers to drink from a dripping faucet or from running water, with the bird-bath as a last resort. He did not recall ever having seen a Lawrence goldfinch drinking from a faucet, but it visits a quiet pool or basin. This difference may not be true at all localities, but he noticed it for a number of years at Azusa, where both species are abundant in the spring and early summer months.

Edwards (1925:78) has described the behavior of goldfinches at a bird bath. Early in January she set a Potter trap over a bird bath which had water, about four feet off the ground, hoping to get some of the many green-backed goldfinches and pine siskins that come in flocks to the water. In a short time a flock drifted in and three of the goldfinches and a siskin were caught, two in each end of the trap, while the rest of the flock of more than 50 birds crowded over the trap and bath mound, chirping cheerily. On approaching the trap to remove the captives, the greater part of the flock remained at, and around, the far end of the trap, not 2 feet away, and stayed during the removal process, scolding her and looking at the birds in the trap and trying to get at the water. She reset the trap several times, repeatedly catching more birds before she could finish banding the one in hand.

The birds virtually covered the trap and rock sides of the bath, flying from it to the near-by fence and back again like a swarm of bees. Suddenly they were off again, leaving the yard as quickly as they had come. Another day, while banding a siskin just trapped at the bath, two of the goldfinches flew in and alighted on the closed trap, chirping vociferously. When the trap

was reset, they retired to the fence. Then they immediately flew in, had their bath, and were banded. Mrs. Edwards banded 26 green-backed goldfinches in the months of December and January.

E. D. Clabaugh (1930) reported that in his bird banding, green-backed goldfinches were captured only by using water as bait. Both the Warbler and Potter traps were used, generally with water dripping into the trap in some manner. It is well to set the trap near some seeding annuals such as cosmos or coreopsis.

In a garden in Santa Barbara after the rainy season of 1904-05, Mailliard (1906) studied the abundance of birds in early summer. Later in the season water became scarce, and the birds eagerly sought artificial pools and small amounts of water in Indian mortars and from dripping hydrants. It was usual to see a line of green-backed goldfinches awaiting their turn to hang upside down on a faucet and let the cooling water fall into their open bills, drop by drop. And often the drops came slowly. At one place a brown towhee would keep possession of a water source and prevent the small birds from gaining access to water. Sometimes, a thirsty group of goldfinches waited impatiently in a bush overhanging the bowl. If they dared to approach, the towhee would attack them.

At midmorning on January 10, 1954, at the Hastings Reservation, a flock of juncos and goldfinches was at a water trough where the water was covered with ice. At one corner there was a pool where the ice was melting and two goldfinches drank there. A male goldfinch was standing on the ground beneath one corner where it ruffled its feathers and attempted to bathe. Later a goldfinch moved over the frozen surface from one edge of the tank to the other. An hour afterward the flock was back at the trough and many of the birds drank.

Before noon on January 6, 1949, green-backed goldfinches began coming to water at a trough. There were two to seven at a time. Following repeated trips to drink there was behavior in which one bird, after drinking, would reach its neck and head toward another a few inches away; then usually both birds quivered their wings, uttered what seemed to be strident begging calls, and worked their bills together as if one fed the other. Dull-colored birds approached both dull and bright and the reverse was seen. Several times the stationary bird flinched away as if it had been threatened by the approaching bird extending its head and neck. Newly alighted birds were approached more frequently than were birds which had been at the trough even a few seconds. One at a time birds a few inches away came up to new arrivals. Four birds clung to twigs and drank from 2-inch thick ice near the trough and melting in the sun. The birds drank readily from the 2-inch wide sheet metal, a continuation that bordered the sides $1\frac{1}{2}$ to $1\frac{3}{4}$ inches above the water. Two birds drank from a dead $\frac{1}{2}$ -inch diameter, horizontal, curving twig at a point $3\frac{1}{4}$ inches above the water. This necessitated leaning forward with a firm grip on the twig so that the tarsi were horizontal. The observer saw none of the birds slip. The birds, in small numbers, were still in the vicinity at 11:53, when several drank.

Early on April 16, 1940, at the Hastings Reservation six goldfinches were in a creek drinking and bathing. During the dry season the green-backed goldfinch is dependent on water, and for that reason it is not able to range

as widely as it does during the wet season, when the flocks may be found in the heart of the chamisal. The birds present on the Reservation at the end of May were not in flocks. They probably reassemble as the nesting season ends and as they are drawn to the same spots by their need for water.

Early in the afternoon on June 8, 1939, a female and an immature goldfinch drank at a water trough. They flew to the shade of a valley oak and were replaced by a female and a male. All the birds lit at the shady end, but because they were unable to reach the water there, they would sidle along to about halfway from the end. The male reached the water from a greater distance. The shaded end possibly provided more protection for the birds. In a cloudy morning on June 14, 1939, a male goldfinch flew to a water trough to drink. On the previous day in sunshine, the birds had gone to the shaded end first.

At 8:30 A.M. on July 12, 1939, many green-backed goldfinches visited a short section of running stream. The main purpose in coming was to drink; as many as seven or eight were drinking, crowded together along the edge of the water. They appeared to go down to the water in groups rather than singly as if this manner provided a safety device. A group may be more likely to detect approach of danger than a lone individual. In early afternoon a female goldfinch came to the edge of a creek and drank. She dipped her bill eleven times. At 9:30 A.M. on July 23, 1946, three birds were seen on a creek as they flew down to drink from stones above the water level. Beginning around 9:00 A.M. on July 24, 1939, many goldfinches came down to drink in a short section of running water. They arrived singly, in twos, and in small groups. They lit in live oaks and in tall dead sycamores. Late in the morning a pair of goldfinches came to drink, not to bathe. They spent half a minute at the water's edge, then left. At 6:30 A.M. on July 29, 1942, a pair was on the stones in water, drinking from a creek. Each bird dipped its bill, then elevated its head to swallow. The male did this five times; the female about as many. In midmorning on July 31, 1939, one green-backed goldfinch was dipping its bill into water, then working it up and down as if bringing up pap.

At 6:20 A.M. on August 3 five goldfinches came to the stream below a water tank to drink and returned within 15 or 20 seconds to a live oak. From there they flew down the slope. On August 10, 1939, flocks were larger than a week earlier, but this may have been only temporary assembly while drinking. At 10:15 A.M. a flock of about ten birds flew downstream to drink about 20 yards below a bridge. After spending about 2 minutes in bordering willows and at the water, the group left in flight. Between 12:15 and 3:00 P.M. two birds watered at a spring. They side-stepped down a near-by vertical willow twig projecting into the water, in order to drink. At 6:30 A.M. on August 16, 1949, goldfinches drank until 6:55 when they came from all parts of a willow and started converging on the trough edge and dead willow twigs within 18 inches of the trough. As soon as a bird reached the edge of the trough 1 inch above the water, it began to drink, dipping into the water four or five times before flying away or being forced out by the movements of other goldfinches, brown towhees, or juncos which were drinking at the same time. Little or no bodily contact occurred, especially between species, a simple quick movement of the body by the towhee being sufficient to scare

off three or four goldfinches. In leaving they would fly to open branches in the willow 6 to 10 feet away. At one time ten goldfinches were lined up together, shoulder to shoulder, drinking from the end of the trough where the water was closest to the edge. One goldfinch drank by clinging to a willow branch $\frac{1}{2}$ inch in diameter, a full $2\frac{1}{2}$ inches above the water.

In the late afternoon on September 1, 1938, seven goldfinches lit at once, and others were in the moist opening where a water tank overflowed. They obviously searched for water as they perched in the ceanothus. At 10:30 A.M. on September 6, 1939, the overflow pipe from a well led to a barrel set on a creek bed under a red willow. The barrel was full of water. The water pouring into it overflowed so that one edge was wet and the other was dry. Numerous goldfinches were in the surrounding willows. After a few minutes they began to come to the barrel to drink, unlike the juncos which drank from the creek bed. The first one landed on the edge. Then in 3 or 4 seconds two more followed until finally as many as eight were lined up drinking, and the first ones started to fly off. All the birds drank from the wet edge, not one from the dry edge. Numerous hornets were about the barrel, but there was no interaction between them and the birds. One goldfinch, on approaching the barrel, knocked a bird already there into the water. The observer thought there was no physical contact; rather, the drinking bird, sensing something behind it, brushed into the water in its haste to fly off. Although not all of the birds stayed on the barrel at the same time, most of them moved into the willows closest to the barrel.

At midmorning on September 7 many goldfinches were seen and heard in the coast ceanothus, attracted by the overflow of water. As many as thirteen were standing and drinking in the running water within a radius of 1 foot. When frightened they flew into the ceanothus. Thence they went downhill 10 yards where they reassembled at the water to drink again in a compact group. Six came out of the ceanothus and flew away. Three came in and two dropped deep into the brush. In midmorning on September 11, 1939, a compact group of seven or eight goldfinches perched on the edge of a trough to drink. Fifteen minutes later the same group was drinking at the same place. Late in a morning in mid-September goldfinches were drinking only from that part of the water trough which was in the shade or semi-shade. However, that part was also closest to the water. In the afternoon twenty were drinking. Something frightened them, and they all flew off into the nearest trees, except one which remained, continued to drink, and probably was the attraction for the immediate return of the others. All again drank at the same spot. At 9:10 A.M. on September 17, 1939 a small flock was about a water trough. Later in the month many drank at a water trough in early morning.

At 10:45 A.M. on September 27, 1946, after about 5 minutes in the vicinity of a water trough along a creek, an observer estimated that at least fifteen goldfinches were in willows within 30 feet of the water. In the previous weeks these goldfinches had been close to water almost every time a watering place had been examined on the Reservation. In early morning on September 30 green-backed goldfinches visited a spring. Six came on the last trip. About the same number was observed on the two preceding trips. On each trip

they followed the same route through a willow, into a live oak, and down through the outer branches of this live oak about 10 feet to a pipe, dripping water. The goldfinches drank from this pipe by standing on its edge, bending over and picking at the water drops before they fell from the pipe's lower lip. At 9:25 and 10:00 to 10:10 A.M. about ten goldfinches came to the outlet to drink. At 9:30 A.M. one was drinking from the end of the pipe when a brown towhee flew there to drink. The goldfinch left the pipe when the towhee was about 6 inches from it. At 11:05 A.M. on October 4, 1939, twenty goldfinches were at a water tank bathing and drinking at the overflow of water and sunning and preening in ceanothus. On October 11 about 25 flew along an overflow and into coast ceanothus from which they hopped down to drink. At 10:20 A.M. on October 12, 1939, fourteen goldfinches came to drink at a creek. They alighted in a bushy willow and went down to water individually, not as a group. One male *S. lawrencei* was with them, without a female. A golden-crowned sparrow came to drink and was not disturbing. After drinking, the birds moved about the willow. Four of them left, and then a group of eleven others flew in a different direction. The air was hot that day. On October 15, the overflow from a water tank started to run at 10:35 A.M. At 10:40 A.M. fifteen goldfinches, that had been in the ceanothus 10 to 20 yards below the water tank, appeared in the live oak beside the overflow pipe. Apparently they wanted to utilize the water, the sound of which must have attracted them, but they were afraid because the observer was only 10 feet away. They perched on the branches directly above the water. Within 2 minutes one flew to within 6 inches of the water, hovered, and flew back to the oak. Other birds repeated the attempt, but none lit on the ground for 1½ minutes. After one succeeded and, standing in the water, began to drink, the rest came down within 15 seconds. All drank for 4 minutes, without bathing, and then flew downhill. They did not reappear for 15 minutes.

At midafternoon on October 18, 1939, a male and female were drinking at a water trough. Five minutes later one male, with six Lawrence goldfinches, was drinking at a water trough. At 10:00 A.M. on October 19, two males and two females perched 20 feet up in a valley oak before going to drink at a trough. On October 21, despite heat and high wind, few birds were coming to a water tank overflow. The small groups of three to five individuals, did not stay long. At 9:45 A.M. on October 23 some birds in a mixed group of goldfinches were drinking at the junction of two creeks. On October 31, 1948, between 8:20 A.M., shortly after the sun struck a water trough, and 10:00 A.M. when the observer left the place, a flock of goldfinches was almost continually present in the willows and drinking at the trough. Not more than five were on the trough edge at once, but at least forty came to it. There were fifteen or twenty in the willows at one time, but apparently two or three flocks were represented. One group of six or eight arrived about 9:10 and the observer saw five as they dived from a hill straight down 25 feet into the top of the highest willow. The movement away from the trough was generally downstream.

In midmorning on November 2, 1945, eight to fifteen goldfinches at the same time were on a fence above the trough. Usually they never went directly to the water, but they stayed in small groups of four, or six, birds chattering

in a low voice. One male took ten gulps of water and then flew away. A female took eleven drinks as the observer watched. On November 4, 1937, one goldfinch was at a spring, drinking from the dripping end of a pipe. A few minutes later another one arrived there. In late afternoon on November 15, 1939, seven birds at a water tank drank and bathed in the overflow. At 9:15 A.M. on November 28, 1937, a group of goldfinches at a spring began to assemble in a dead blue oak and in dead sycamores close by. When about fifteen had come, by twos and threes, they perched, preened, and picked at the limbs for about 10 minutes and then, one at a time, went to the dripping pipe to drink.

Before noon on December 15, 1946, a male flew from willows to a fence above a water trough. After pausing there less than a minute it flew to the trough to drink. About 30 seconds later this male flew out of sight up the canyon.

At 1:00 P.M. on January 6, 1945, twenty goldfinches called in willows at the edge of a creek. Below, in shallow water in the creek nine more bathed. The water reached partway up on the flanks of each bird as it stood, frequently dipping the head and vigorously shaking the feathers and body, making drops of water fly in all directions. Other birds frequently joined the bathers. Individuals in the water frequently flew up to near-by willow branches to shake their feathers and to preen. Once, when ten goldfinches bathed, a pine siskin joined them for a short period and bathed. One female goldfinch remained in the water and shook herself about every 3 seconds for 26 seconds. The average time each bird remained in the water was close to 15 seconds. A continuous chorus of calls was audible from birds in the willows, birds bathing, or both.

Before noon on April 6, 1939, a goldfinch flew into a live oak from a creek, where it had been in the water. It shook itself, flew back to the creek, lit near the water, and then waded into the center of the small stream, put its beak and head into the water up to its eyes, squatted, and fluttered its wings, splashing water over its back. It bathed thus for 2½ minutes, stopping every 5 or 10 seconds to utter a *cheep* and to rest. It flew from the water to a near-by exposed dead branch, shook itself several times, and flew into a live oak where it shook itself again, preened for a few seconds, and flew away. On May 11, 1939, several goldfinches were drying plumage after bathing in a creek. Late in the afternoon on June 21 a male was drying plumage in the sun on a dead bush after bathing in a creek. In midmorning on July 31 six goldfinches were bathing in a pool 9 x 12 x ¾ inches. They dipped the breast and neck in the water, fluttered the wings to throw water over the back, and fanned their tails. They bathed with a 2-inch gap between each two, but not closer than that. There was no fighting. If a bathing bird crowded another, one moved away, usually the one that was the least active. On the morning of September 1, 1939, most of the bathing was in the sunshine, probably because of the cool wind and overcast sun. In late July no choice between shade and sun was noted. On September 8, 1942, at 8:30 A.M. 15 birds were seen 40 yards down the creek, where it was sunny and warm. Many were preening wet feathers after a bath, and some were chasing one another in flight. Three weeks later at 8:00 A.M., half a dozen gold-

finches, including at least two adult males, bathed in a spring. They were drying, preening, and piping in adjacent willow clumps.

In midafternoon a flock of eight flew to a dead bush by a spring on a south slope. All clung sideways to dead branches for 10 seconds, and then flew down to the spring. Each bird drank several times by dipping the bill in a shallow puddle and then tilting the head back. Two hopped to the middle of the puddle ($3 \times 6 \times \frac{1}{8}$ inches) and tried to bathe. There was much fluttering of wings, scaring others away, and fluffing out of feathers. After 5 seconds each bird flew 150 feet to the top of a chamise bush and proceeded to preen and shake the feathers in the warm sun. Between 3:00 and 3:30 P.M. eighteen birds came to drink at this spring. The flock chattered a great deal. At 8:15 A.M. on November 10 a flock of ten birds preened and dried plumage in the sunshine, in an elderberry bush beside a creek. Evidently they had just bathed in the creek. One attempted to bathe in a water trough. The water was about an inch and a half below the edge of the trough and the goldfinch had difficulty in reaching it. The bird reached down and touched the water with the side of its head, and then it turned sideways and fluttered, clinging to the edge of the trough.

By July 31, 1939, water was not running in some regular watering places. Four goldfinches were driven from one place and one from another, by a female Bell sparrow which lunged at them. They were in mud of a drying overflow channel. Previously they were not pursued when the stream was running. On August 2, 1939, five goldfinches began to bathe at 5:50 A.M. in a water tank overflow. All but one flew when a California thrasher came to drink, although it did not threaten them. One remained watching from a spot 10 inches away.

Gregariousness of a group is notable; any bird up to the size of a thrasher, drinking or bathing at a stream, serves as a nucleus to attract several goldfinches, which bathe and drink all about it. After one or two goldfinches alone have begun to bathe or drink, several others immediately follow them. A plain titmouse, drinking, was annoyed by two goldfinches which joined it, and it drove them away, but five others came down and were tolerated. The titmouse left and when it returned, the goldfinches did not fly away at its arrival. The goldfinches were the most numerous birds here and they bathed the most. One goldfinch was pursued by a female Bell sparrow in the drying stream channel, but five others, watching from a bush, came down and were tolerated by the sparrow.

At 4:40 P.M. on August 3, 1939, there was a brisk, steady breeze, warm air, and no flowing water. Two young goldfinches flew at different times to another perch, forcing the bird there to leave. This is in keeping with the practice that the birds congregate about another which serves as a nucleus. No resentment is shown by the dispossessed bird, which always leaves when the other one flutters near it, slowing down for a landing. We did not see a young bird drive away an intruder, but during nesting a female will occasionally chase away a male which comes too close. Goldfinches were not so numerous there that afternoon, probably because of lack of water and a drying, brisk wind from the northwest. Also, the sun was warm on this slope. All the birds flew to shelter in live oaks and later they flew toward a distant

hill. There was not much calling from the birds that afternoon. None was seen in the dry stream-bed.

PERCHING

Between 9:40 and 9:45 A.M. on January 7, 1945, twenty-five green-backed goldfinches perched at the tops of several sycamores bordering a stream. Many call notes were audible. At 6:30 one alighted on a leafless underbranch of a live oak. On September 3, 1946, three goldfinches perched at 10:30 A.M. in the top of a live oak. They paused in the top of this tree less than a minute; then they flew up the slope of a hill and out of sight. On September 6, at 9:50 A.M. at least twenty perched in the willows bordering a creek. In midafternoon on September 15, 1939, a goldfinch remained on a perch 1 minute and 35 seconds; there was no observable cause for flight. Another goldfinch remained 35 seconds; then it flew when a bird passed within 4 feet overhead. Another stayed 16 seconds, and then flew to the place where the main flock had alighted. Still another remained 3 minutes and 58 seconds before it flew off with two others from a flock of fifteen.

Near noon on May 21, 1939, a male was perched high in the top of a 40-foot willow. The bird cleaned his bill but he did not preen. He remained there in the sun more than a minute and then flew over the trees. The goldfinch was not disturbed by a solitary vireo that foraged 4 feet from him. At midday a goldfinch was in the top of a tall dead sycamore beside a creek and perched in the hot sunlight. Three more goldfinches arrived and perched near the single one. Two birds flew down to live oaks and then to a water hole. The other two rethained in the sun, wiping their bills and cleaning their feet.

In midmorning in late July many goldfinches came to drink at running water. They arrived singly, in twos, and in small groups. Mostly, they lit first in live oaks or in dead, tall sycamores. In midafternoon in late September, 1939, two goldfinches perched on the tip of a live oak rising out of dense chamisal.

ROOSTING

At the Grand Canyon, Arizona, Townsend (1925) saw 24 green-backed goldfinches settle for the night in a cottonwood, still in leaf and close to the back door of his cabin.

Sleeping habits of the green-backed goldfinch have been studied by Comby (1944) who reported that

A male green-backed goldfinch chose as a sleeping perch a tree tobacco plant (*Nicotiana glauca*) in my yard, on San Jose Creek, near Whittier, California. He was seen to roost there daily throughout most of January and a part of February, 1944. Each evening he came to the plant early, about an hour and a half before sundown. Here he slept for twenty nights, January 10 to 29, inclusive, but was not to be seen on the 30th or 31st. A light shower or drizzle on the 30th may have been a disturbing factor. He returned to the plant on February 1, to remain through the 16th, although toward the end of this period he came later, just before dark. This was the only individual of the species to perch in the shrub or to be seen in the neighborhood at this time of day except for two or three occasions when another individual alighted momentarily in a near-by tree tobacco. Although the male goldfinch used the same plant for sleeping, he did not always rest on the same branch or face the same direction; his position varied, it is estimated, from $4\frac{1}{2}$ to $5\frac{3}{4}$ feet from the ground. Like many other birds he slept with head tucked 'under the wing'.

The first season's growth of this plant retains its succulent leaves and stems throughout the winter. The yellow-green bird was well camouflaged in the yellowish-green foliage, and careful inspection was necessary to distinguish it; discovery of the roosting place was made as the bird flew into the shrub.

At the Hastings Reservation we have studied the roosting habits of the goldfinches. Besides the regularity of the daily schedule there is a seasonal regularity in the choice for certain roosting trees. Each evening in late September, 1952, several goldfinches gathered at dusk in a locust tree as if in preparation for roosting. On October 18, 1944, the goldfinches began to stir on roosts at the top of a sycamore at 6:02 A.M. At first only scattered thin calls were uttered. At 6:05 a male flew to an exposed twig at the top of the tree. At 6:15 the birds first began to fly about the trees in the vicinity, and there was much chattering. At 6:07 on October 27, 1948, there was some activity in the dense foliage of a live oak. When the observer passed under the tree, eleven goldfinches flew out. They were evidently just leaving their roost in the tree. On October 28, when there was a high fog before daylight, a flock of about twenty goldfinches left the southeast side of the large live oak at 6:24:50 A.M. Two or three others remained in the tree. The flock flew southward, turning from side to side and with a turbulent mixture.

At 7:25 A.M. on January 9, 1945, a loud, continuous chorus with a variety of calls issued from the interior of a large live oak. No birds could be seen. These goldfinches roosted nightly in this tree. Although it had been light for half an hour, they had not yet left the tree. At 5:15 P.M. on January 14 a chorus of calls was uttered from the large live oak. At 4:49 P.M. on January 18 thirty goldfinches flew out of the live oak. Before the observer disturbed them, he could hear a chorus of calls. All flew out from dense clusters of twigs. They had begun settling for the night. They flew out 200 feet and returned to the oak after the man passed by. Males and females seemed to be present in about equal numbers.

During the 10 days to 2 weeks before February 10, 1945, the goldfinches left the vicinity. A flock of twenty-five had been roosting in a live oak each night and many could be seen during the day on near-by trees. In early February not a single goldfinch was present.

At 6:10 P.M. on September 1, 1949, about fifty green-backed goldfinches milled noisily in and about a 60-foot live oak 40 feet from a water trough. The birds hopped about and flew between clumps of leaves and to and from near-by live oaks and willows; many of them kept up an almost continuous chatter which the observer had not heard from them. This frantic milling, aside from strictly gregarious pursuits, chasing one another about, hopping along in twos and threes, and noise, was a prelude to selecting roosts for the night. This procedure, judging from the amount of bustle, fuss, and noise involved, seemed to arouse a great deal of needless competition. There were many more good roosts in this tree than were needed for the birds. One bird settled for the night at 6:35 P.M. It had followed another bird to this spot, apparently tried the site momentarily, but immediately it hopped on out of sight while the second bird hopped onto the $\frac{1}{4}$ -inch twig, ruffled its feathers slightly around the shoulders, preened once on the left side of the breast, and settled close to the twig with a brief "double" shake. This position was on a

horizontal twig out in the peripheral leafy canopy 45 feet above the ground. A small opening among the leaves, about the size of the bird, afforded a view from below, but leaves only $\frac{1}{2}$ or 1 inch away on the sides and above shrouded it securely.

Another bird settled in a position at the edge of the canopy 6 feet above the ground on a $\frac{1}{8}$ -inch twig enclosed on all sides except the head, by leaves. The head was in such a position that it had a good view out toward an open area. By careful scrutiny at close range (2 ft.), the observer could make out its feet lightly clasping the twig. When he was standing this close, the bird stood with legs extended, but no doubt the roosting bird drops its body closer to the roost. At 6:40 nearly all the sounds from the birds had ceased, and only a few birds still flitted and hopped about in quest of a roost. At 7:00 P.M. all the birds were quietly situated on roosts. Most of them roosted in one tree although some of them had been flying out to near-by trees, 15 to 30 feet away and going through the same noisy procedure although most of them seemed to return to the central tree.

At 5:55 A.M. on October 19, 1944, the birds were just beginning to stir in the trees around headquarters. At 6:10 a flock of goldfinches was beginning to flutter and chatter in a 20-foot valley oak on the south side of a hill. At 6:03 A.M. on October 23, six goldfinches began chattering from high up in a sycamore. At 6:00 A.M. on October 27, ten goldfinches chattered from the top foliage of the sycamore. At 6:08 A.M. on October 30, ten began chattering from the top foliage of the sycamore. At 4:45 P.M. on November 9, 1937, as a man walked beneath a large sycamore across the road from a barnyard and a water trough, after sunset and when it was beginning to get dark, several goldfinches suddenly "exploded" from the thick foliage over his head, twittering as they flew. They flew up into the higher part of the tree. Evidently they had settled for the night, roosting near together. Numerous excreta were found near the places the birds had left, and on the ground beneath, indicating that this roost was used regularly. Two of the birds flew to a near-by live oak. When the observer moved away, the birds almost immediately returned to their original perches in the sycamore, about 10 feet aboveground where a densely branching limb projected downward and provided sheltering foliage on all sides.

The next evening at 5:00 P.M. the observer investigated the sycamore limb where roosting goldfinches had been flushed the previous evening. As he approached, two goldfinches flew out. When he walked beneath the tree, another left, and when he shook the limb gently, two more darted out from among the leaves. All came from points within a foot of one place, but it was evident that they were not in actual contact while on the roost.

At 4:20 P.M. on November 11, 1937, a goldfinch flushed from its roost in a live oak, where it had settled for the night. The bird was about 10 feet from the ground in the long pendant outer branches of the tree, in thick foliage and twiggery. At 5:00 there were no goldfinches roosting this night on the limb of the large sycamore where several had roosted near together for two nights. At 4:40 P.M. on November 12, 1937, several goldfinches fluttered about in thick outer foliage of a live oak, apparently seeking a place to roost. After several minutes the fluttering gradually subsided, and the birds gave low, piping notes like contented young chicks.

At 6:00 A.M. on November 5, 1944, ten goldfinches began to stir near the top of the tall sycamore. At 6:15 A.M. on November 11 six goldfinches called from the tops of trees in a yard. On November 15 at 6:38 A.M. about thirty goldfinches flew up from the top of the sycamore and out of sight up the canyon.

At 6:55 A.M. on December 16, 1944, as a man walked under a live oak beside a creek, six goldfinches flew out from dense twigs and leaves where they apparently had roosted the previous night. At 5:15 P.M. at the same place several birds had fluttered about in the leaves and twigs, and uttered several notes, but they did not fly. At 5:15 P.M. on December 18 as the man walked under the large live oak at the edge of the creek, ten goldfinches flew out from dense leaves and twigs 6 feet aboveground where they already had gone to roost.

SUNNING

On August 24, 1949, a male and two females perched in the bare top branches of a tall sycamore. They sat quietly in the sun for at least 5 minutes before being joined by four more, one of which was an adult male. Five of the birds ruffled and preened in the next 3 minutes before the group flew off upstream in smaller groups of three, two, and two, at 5:20 P.M.

PREENING

On June 11, 1939, at 11:03 A.M. a male goldfinch cleaned its toes with its bill. In 5 minutes it cleaned both feet. The bird probably had perched on some sticky plant. The middle toe of each foot required the most care. The bird cleaned its bill on the branch of a tree during and after the process of foot-cleaning. In mid-August five goldfinches preened and rested in willows at 9:50 A.M. for 15 minutes before moving downstream.

FLOCKS

The goldfinches are gregarious. They like to assemble with others on the same bush. If frightened, which is a frequent occurrence, all fly off together; but in no cases did we see all of a group land together. Rather, some fly straight ahead, others turn to the right or left; some land on bushes, some on trees. They scatter as a thrown out handful of sand. If a bird finds that he has landed on a spot without companions, he generally flies to a place where other goldfinches are concentrating. The individuals in a flock coming from a distant point are likely to land at the spot where they see a concentration of their fellows. The flocks, pairs, and individuals wander widely in response to feeding sites, nesting locations, to find water, and to roost. These travels are controlled by the climate and the weather. The birds are small and inconspicuous under certain conditions. Flocking becomes prominent when the birds assemble to forage and congregate at sources of water.

From mid-June to mid-July, 1946, goldfinches were seen in groups that fed on the abundant seeds then maturing. The many young birds joined in the flocks. They also frequented watering places. Early in July there was a marked reduction in numbers in the places frequented through the spring and summer. This followed the drying up of many of the plants on which they fed.

In July and August, 1950, a small group of six or eight goldfinches regularly perched in a live oak that stood beside a drain from a house. The birds were attracted to the water. At midday on August 27 when the temperature was higher than usual, these birds sang in chorus continuously, deep inside the foliage of the large live oak. From 4:30 to 5:30 P.M. on August 10, 1948, three flocks came to drink at a water trough. The first flock contained at least a pair of adults and four or five juveniles. The second contained mostly juveniles, and a Lawrence goldfinch was heard with them. The third, at 5:30 P.M., consisted of about twelve juveniles, with at least one adult male. From 5:30 to 6:30 P.M. on August 29, 1948, a large flock of goldfinches, in which there were no adults, was on a creek. At first the birds were silent, and they collected in small groups in a live oak upstream, coming in from high in the air. Some fed on dead twigs of a willow or a coffeeberry bush, picking something off them, 1 or 2 feet aboveground, but the observer could find nothing they could have been eating, for the twigs were bare. Around 6:00 P.M. the birds began to call.

In the morning on October 20, 1939, an observer watched a flock of more than sixty goldfinches foraging on an open hilltop. When disturbed, the flock flew up, circled, and generally returned to the same spot. The birds frequently alighted first on the deerweed, which, being taller than the grass, or vinegarweed, afforded a better view of the surrounding terrain. At 8:00 A.M. on November 26, 1949, about 100 goldfinches foraged in an open field, or they sunned in two blue oaks at the edges of the woodland. One group of thirty-five contained a Lawrence goldfinch. At 1:30 P.M. on January 21, 1942, two goldfinches came down beside a creek. This species had been seen rarely during the previous two weeks, and never more than two at a time. In late afternoon on February 5, 1938, between 300 and 400 goldfinches perched in tall trees about a barn. Many sang and most of the birds perched in the tops of bare valley oaks; some foraged in outer branches of a live oak. Early in the morning two days later a flock of eight landed in a ceanothus bush 15 feet in from the edge of chamisal. Within a minute all of them left, one by one, except for one group of three. Scattered individuals or pairs perched in a patch of chamise.

At 11:00 A.M. on February 19, 1942, a flock of about eighteen goldfinches flew up a ravine to a leafless buckeye preparatory to bathing and drinking. Members of the flock seemed to be rather loosely associated. A male and female, for instance, flew off together into the chamise, independent of the others, and only three to five went to bathe and drink at the same time. Before dusk on March 1, 1938, a cloudy day, four goldfinches flew into the middle branches of a live oak. They perched for 4 minutes and then began to move about. Within a minute they were again settled, 12 feet above the ground and 3 to 4 feet from the outer part of the tree. They stood with feathers ruffed and heads pulled in. When the observer moved slightly, 20 feet away, the birds flew out and into another live oak 100 feet away.

In northern California where green-backed and American goldfinches were foraging in the same weedy fields, even in close proximity, the individuals of the two species, on taking flight, formed separate companies and kept apart until, when re-lighting, chance might bring them together again (Grinnell, Dixon, and Linsdale, 1930:404).

In the Colorado Valley near the Needles, in early March, Grinnell (1914a:165) found large flocks congregated in the central parts of extensive dense mesquite thickets where, perched from 3 to 4 feet aboveground, they were certainly safe from marauders; here they sang volubly in chorus until dusk. At Twentynine Palms in southern California from October 17 to November 15, 1934, small flocks were present daily in plants of *Wislizenia* (Carter, 1937).

A flock of 100 green-backed goldfinches that I watched at 3:30 P.M. on February 10, 1929, was on the west side of a hill north of Berkeley. Several times most, or all, of the birds flew up and changed position in a compact flock. They did not go down together but they settled in groups. Usually the birds lit first in leafless tops of bushes. One group went down in bushes less than 20 feet from the observer. Most of these birds perched on the bare twigs, picked at their feathers, and preened. One at a time they moved to heads of dead weeds and picked out seeds. Several individuals of one group in a bush were busily drawing the sides of their bills over the stems; apparently cleaning them. The feeding birds kept making single notes with a twittering effect. Once, a flock suddenly and with a miniature roar of wings flew out from a clump of bushes at an acute angle from the ground. Before they had gone 100 yards a sharp-shinned hawk appeared in view, flew to, and perched in the center of the bush the birds had just left. The goldfinches settled 150 yards away and remained for 5 minutes while the hawk kept its perch until disturbed by approaching persons. A foraging flock of goldfinches permitted an automobile to pass within 30 feet, without appearing to pay any attention to it.

CONFLICTS

At 5:50 A.M. on July 31, 1939, a fight occurred between two young goldfinches in the top of a coast ceanothus; both leaned toward the other and opened the bill, meanwhile fluttering the wings. One then flew away, leaving the other in possession of the perch. This behavior may have been an attempt by each bird to beg food from the other juvenile. At 9:00 A.M. on August 30, 1942, two female green-backed goldfinches and a male perched in the top of a 30-foot live oak. Some conflict was apparent between the sexes. One female made a move toward a male and he left his perch for a lower one. Then both females made for him and drove him up a creek.

FLIGHT

The long flights of a goldfinch are undulating; each stroke of the wings bearing the bird upward, and alternating with an instant of downward drop while the wings are closed.

Goldfinch flight is varied according to the species and the circumstances. The rate of flight and the path traced are modified according to needs, such as display or pursuit by predators. The birds may be silent in flight or they may produce calls that characterize the species. The birds move from place to place in flocks or singly. The flight may be a pursuit by one bird driving another. A prominent trait to follow small birds in flight sometimes makes mixed species in the flock. The birds may display plumage char-

acteristics that are striking when the feathers are spread to show patches of color.

A pair of goldfinches, feeding in a barn lot, flew up when a flock of house finches flew over. The goldfinches flew 6 feet above the ground, lower than the house finches, which were 10 or 12 feet high. The goldfinches veered off after flying 20 feet. A group of goldfinches which had been calling in the willows near water took to the air and flew close together, within a space of 6 feet. The next morning solitary birds were seen in the vicinity of a barn lot, one in flight to the west, another perched and calling on top of a sycamore. In early August, occasionally one goldfinch pursued another, and both disappeared zig-zagging through the bushes in flight. Only the young birds were observed doing this. Probably this is a form of play. In September two goldfinches, male and female, on the tip of a blue oak flew off, one chasing the other in a looping, undulating flight for 6 seconds. Both alighted 6 inches apart on the tip of another blue oak. In mid-afternoon on October 17, 1944, a flock of green-backed goldfinches flew off with a rapid flight made up of quick bursts of wing beats and shallow 1-foot undulations in which each bird glided for several feet.

In midday on January 6, two goldfinches lit in the top of a live oak; the trailing bird was a male. Late in the morning on January 20, 1939, a flock of about ten birds flew in close formation. On long flights goldfinches are likely to perch briefly in the top of a tree and then continue on their way. An example of this was observed in early afternoon on March 28, 1946, when two birds lit for about 2 seconds in a madroño before resuming their flight down a ridge. At 4:30 P.M. on July 19 a dark-plumaged male sang on the wing in a small area not over 50 feet across. The flight traced shallow undulations. The dips were 10 to 15 feet long with wing beats at the top of each glide. The white patches under the wings showed conspicuously in flight. On other such flights there was a note between peaks of the dip. The bird closed the wings momentarily at the beginning of the dip and then beat them rapidly to gain momentum. In early September two birds flew from a bush, one 6 to 12 inches behind the other. At first the flight was slow and looping. When the birds came close together, they zig-zagged rapidly up and down.

ASSOCIATION WITH OTHER BIRDS

Goldfinches are associated with numerous kinds of birds. On the Hastings Reservation this involves varied relationships. Predators are prominent in keeping the single birds or flocks on the alert to avoid capture. An opposite response causes the goldfinches to join flocks or single birds that share their habitat. Examples show a wide range of variability in this habit.

At 8:20 A.M. on October 10, 1939, two goldfinches followed a group of Mexican bluebirds as if for company. Two more foraged with a white-crowned sparrow group in shade along a lane.

In midafternoon on November 6, 1944, six goldfinches foraged on a dry flat on a hillside. In an area 100 feet square there were Mexican bluebirds, goldfinches, juncos, house finches, and Audubon warblers. At 2:45 P.M. on November 18, 1944, many goldfinch calls were audible. House finches, juncos, lark sparrows and white-crowned sparrows were also present. At 9:20

A.M. on January 19, 1945, four goldfinches fed at one bush with three pine siskins. At another, three goldfinches fed with two juncos. The goldfinches frequently flitted from one bush to another. Golden-crowned sparrows and one Bell sparrow also fed on chamise. Members of all five species concentrated within a 50-foot square of chamisal.

Accipiter cooperii (Bonaparte).—At 5:32 A.M. on June 13, 1942, a male green-backed goldfinch came within 3 feet of an incubating female Cooper hawk and called, repeating musical, canary-like chirps. Three minutes later a goldfinch sang one song from a 20-foot blue oak about 100 yards up the canyon and about 30 yards upslope. The song was a jumble of notes, sung in phrases, each phrase being one note repeated, or one or two notes repeated. There was an occasional chirp that easily marked the singer. In mid-afternoon a male goldfinch again perched 3 feet from the incubating Cooper hawk, but intentionally or not, there was a large branch between him and the hawk all the time. In the morning there was a disturbance at the nest, when the bird tried to capture a goldfinch that had come too close.

At 9:45 A.M. on August 7, 1942, a male and six female goldfinches perched 3 inches above a juvenal Cooper hawk that was giving the food cry near the top of a valley oak. The finches made no attack, but they remained above the hawk as if wary of its presence. Possibly they were attracted by the food cries of the hawk. They uttered flute songs of their own. At 11:00 A.M. on August 10, 1939, five goldfinches were in ceanothus at a watering place. Twittering a great deal, they fled before a passing Cooper hawk. None returned to the vicinity for 3 minutes.

At noon on August 14, 1941, when a Cooper hawk called, a nesting female green-backed goldfinch swung about on her nest, facing southeast. She stopped singing abruptly and appeared rigid. After that, the first movement was 8 minutes later, when she flicked her wings. At 12:40 she pecked at the outside rim of the nest. Then she started the excited chatter, stood up on the nest, left the southeast rim, and with four or five short, rapid notes she headed for a large oak tree north of the nest-tree. Ten calls were heard from this vicinity.

On July 1, 1939, a small group of goldfinches in flight started to perch in a dead-topped willow, but they discovered a female Cooper hawk perched there and they changed their course.

Accipiter striatus Vieillot.—At 6:05 P.M. on August 19, 1948, when a sharp-shinned hawk flew from 40 feet in the air and lit in the top of a sycamore, three goldfinches in the top of the tree flew out repeatedly uttering sharp chirping notes. They flew about above the trees in rough circles, 10 to 20 feet above the top, in undulating flight, as far as 100 feet away from the tree, but frequently over the top of it. The chirping sounds stopped after about 10 seconds, but the flying continued for about 40 seconds, at which time the hawk sailed off. The goldfinches then alighted in the top of the sycamore and called whistling *tee-a* and *tee-ur* notes. At 11:00 A.M. on October 5, 1946, a flock of about fifteen green-backed goldfinches flew into the upper part of a willow when a sharp-shinned hawk left a patch of willows 20 feet from the goldfinches and flew toward them into the flock. One of the goldfinches was singled out and chased by the hawk for 20 feet southeast, 30 feet west, and 20 feet north. At this point the hawk attempted to grab the goldfinch with its talons, but the prey dropped into a willow clump, thus eluding the hawk. The hawk started down toward the willows, but made no further effort to continue the chase. Instead, it flew to the upper part of a large sycamore. During the entire chase no sound was heard that could be ascribed to either bird. When the hawk flew almost on a level into the goldfinch flock, the flock scattered in all directions; some flying up, some deeper into the willow, and three or four out of sight downstream.

The chase was, with the exception of the last maneuver of the goldfinch, almost entirely at a height of 10 feet aboveground. The willow into which the goldfinch dropped to safety was the first bush these birds passed over during the chase. The somewhat triangular-shaped route taken by the two birds brought them within 5 feet of three different live oaks. The hawk might easily have caught the goldfinch had there been no cover available and if it could have continued the chase, for it was easily the faster bird. Each time the goldfinch turned (at 20, 30, 10, and 20 feet) the hawk was almost upon it—within 6 inches. But immediately after the turn, the goldfinch was at least 2 feet ahead of

the hawk because of the slightly slower rate of the latter in turning. Because the goldfinch was obviously trying to escape there were no dips in its flight. It seemed not to be moving faster than when flying from one bush to another without the pressure from the hawk. The first flight of the hawk toward the bird was from the rear. The hawk first tried to capture the goldfinch while it perched.

At 7:05 A.M. on October 21, 1946, a sharp-shinned hawk flew through a flock of goldfinches about 50 yards down a slope. The flock, numbering about twenty-five, left the top of a large blue oak for less than half a minute, then it returned to the same tree. Because the observer did not see the hawk move into the flock, he did not determine whether it captured a goldfinch. When flying from the hawk, the entire goldfinch flock kept a close formation not over 20 feet across.

Falco sparverius Linnaeus.—At 7:30 A.M. on October 6, 1946, a sparrow hawk made a sweeping dive at a goldfinch perched in the top of a live oak. When the hawk came within 4 feet of the goldfinch, it flew about 20 feet and perched on the top of the oak. The hawk then wheeled about and for a second perched near the original goldfinch perch. Then it left and again flew toward the goldfinch, which vanished down inside the crown of the oak. The hawk originally started after the goldfinch soon after it had perched in the tree from the north at about 20 feet above the oak. It changed its original course about 20° when the goldfinch perched in the oak. The goldfinch faced away from the hawk. After the last flight toward the goldfinch, the latter vanished as soon as the hawk left its perch.

Glaucidium gnoma Wagler.—At 5:30 P.M. on June 8, 1945, a pygmy owl had in its talons a green-backed goldfinch that appeared to be a juvenile. The location was in a barn lot where water in a trough regularly attracted many goldfinches.

Calypte anna (Lesson).—At 8:00 A.M. on August 22, 1942, a female green-backed goldfinch dived toward an Anna hummingbird that was perched in a willow. The goldfinch missed the hummer by only 4 inches as it flew away.

Colaptes cafer (Gmelin).—At 10:30 A.M. on October 5, 1939, six goldfinches, including three males, flew to perches in the top of a dead sycamore beside a red-shafted flicker.

Empidonax difficilis Baird.—At noon on July 9, 1939, a western flycatcher came and tried repeatedly to drive away a goldfinch that perched on stems of prickly sow-thistle.

Corvus brachyrhynchos Brehm.—At 5:05 P.M. on September 19, 1944, a flock of about ten goldfinches was in a 25-foot blue oak halfway up the west slope of a hill. They moved about and clung to the twigs at the very top of the tree, occasionally giving thin call notes. When an American crow flew over, 50 feet in the air, it startled the flock and all the goldfinches flew off downslope.

Pica nuttallii (Audubon).—At 9:00 A.M. on July 6, 1941, a goldfinch followed a yellow-billed magpie through a red willow. This was about 15 feet above the ground. The goldfinch made two sallies at the magpie, but it did not come closer than 2 feet away. There probably was a goldfinch's nest close by.

Aphelocoma coerulescens (Bosc).—A flock of fifty goldfinches chattering in a live oak at the end of January momentarily became quiet as a screaming scrub jay came by. At 6:50 A.M. on May 25, 1939, a scrub jay flew to a limb 4 inches from the nest of a green-backed goldfinch. The female goldfinch from the north and the male from the west flew about the jay, not coming closer than 8 inches. They did not touch the jay, but they flew at it and then away; the male twice, the female once. The jay went north, both birds after it, but they did not remain away more than half a minute, when the male was back near the nest. The jay came again at 6:55 and the goldfinches flew around it. The jay perched 6 inches under the nest, the head level with the bottom. It saw the nest, turned around, drove its bill into it on the east side, then around to the west, where it repeated the performance. The female goldfinch flew to a twig $1\frac{1}{2}$ inches away, while the male went in pursuit of the jay as it flew west. Many other birds (5) also in the vicinity were churring at the jay. At 6:58 the male returned, perched $1\frac{1}{2}$ inches north of the nest and flew west again. The jay came to the tree at 7:02, but it did not go near the nest.

The records were discontinued until 8:12 A.M. when the observer arrived and saw the female flying away from the nest. The nest was badly torn; the jay had been back. The southwest side hung loosely, with a hole on the south side. At 9:35 a male goldfinch flew up through the nest tree from the west and to a valley oak 15 feet away. He remained in

the tree $\frac{1}{4}$ minute, and then flew back the same way. He did not go near the nest, which became looser, probably because of the wind. A piece on the south side hung farther and the northwest side seemed entirely gone. The observer left the area at 9:40 A.M. When he returned at 11:00 A.M., he saw no goldfinches. The nest was as before, but loose shreds were beginning to appear on the torn edges. It would go to pieces rapidly. At 11:40 a male came from the west to the tree, perched 5 feet above the nest, and seemed to be looking at it; meanwhile he called: location-note, *mew* note twice, and then flew away.

In the morning on August 10, 1939, a scrub jay swooped within 10 inches of goldfinches in ceanothus bushes, and all of the goldfinches flew out in one group, headed for live oaks.

Near noon on November 5, 1946, at least fifteen goldfinches perched in the top of a sycamore. When a scrub jay flew into the tree and approached within about 5 feet of the finches it caused about five goldfinches to leave the tree. The jay perched on a branch recently occupied by one of the goldfinches and about 15 feet from an additional group of ten goldfinches. Less than 5 seconds after the jay first perched in the tree, it flew toward the second group causing the small birds to leave the tree. Both groups of goldfinches flew to the tops of live oaks about 20 yards from the sycamore.

Parus inornatus Gambel.—At 9:30 A.M. on May 29, 1938, a female goldfinch pursued a plain titmouse once. At 7:15 A.M. on July 27, 1939, a male goldfinch was attempting to drive a titmouse out of a live oak. The goldfinch kept calling the location note, but it was unanswered. It flew at the titmouse, which evaded it, flew 2 feet away, and continued to forage. The goldfinch uttered more calls, then flew at the titmouse again, and again the titmouse evaded it. The goldfinch continued to make the location note, but it was not answered. The titmouse left, but the goldfinch stayed for 2 minutes, calling almost continually. It seemed to be seeking a mate in the nest-tree, but the observer did not see a nest.

In early afternoon on September 17, 1939, there was no bird at a water trough for 6 minutes. Then a titmouse arrived to drink. Immediately a goldfinch that had been twittering in a live oak flew down, and within a minute more than ten goldfinches were drinking. On October 15, 1939, goldfinches had been drinking, but they flew off and did not reappear for 15 minutes. At that time two titmice flew down to drink and bathe. Within 2 minutes the goldfinches drank and bathed in the same spot, although the titmice made no sound.

Sitta carolinensis Latham.—At 9:10 A.M. on July 31, 1939, a white-breasted nuthatch that came to drink or bathe was driven away from an overflow as one green-backed goldfinch came down to the water, fluttering over the nuthatch's head.

Psaltriparus minimus (J. K. Townsend).—At 2:50 P.M. on September 9, 1939, 35 feet below a water tank, bush-tits were bathing. They seemed to attract the goldfinches, for sixteen came to sit on the branches of coast ceanothus and woolly eriodictyon immediately above the spot. They made no attempt to force the bush-tits away, but merely sat and waited. When most of the bush-tits had gone, the goldfinches bathed in exactly the same spot where the bush-tits bathed. At 9:55 A.M. on November 28, 1939, a goldfinch ate chamise achenes, but it was disturbed by a flock of bush-tits, which swarmed uphill through the chamisal all around the goldfinches.

Troglodytes aedon Vieillot.—In midmorning on May 24 a house wren sang in a tree 20 feet southeast of a goldfinch nest; apparently it caused the goldfinch to swerve toward it. At 6:30 A.M. on August 16, 1949, while seven or eight green-backed goldfinches drank, a house wren started a slow, loud rattling noise which caused them all to retreat to the willow 8 to 12 feet away. The wren was soon joined in this noise-making by another house wren deeper in the base of the same willow. The continued noise caused all the goldfinches to flee from the entire area; most of them flew into red willows 50 feet farther upstream.

Toxostoma redivivum (Gambel).—At 9:10 A.M. on July 31, 1939, a whole group of goldfinches at a small pool in turn was driven away as a California thrasher came to drink, although it did not threaten. At 8:30 A.M. on August 2, 1939, three goldfinches bathed and drank within 6 feet of a thrasher which drank in the stream. There was no disturbance. The cause of their alarm, when the thrasher came earlier, evidently had been a quick lunge as the bird darted out from under the bushes.

Sialia mexicana Swainson.—About 8:15 A.M. on August 11, 1939, a goldfinch ate green fruits from honeysuckle. It flew off following a Mexican bluebird. About 8:30 A.M. half a dozen goldfinches came with several bluebirds and lit in a redberry bush. At 4:00 P.M. on October 4, 1939, three goldfinches followed a bluebird as if it formed a nucleus about which they could flock with safety. At 8:20 A.M. on October 10, 1939, two goldfinches were following a group of bluebirds, apparently for company. At 4:17 P.M. on October 22, 1944, when seven bluebirds flew over a canyon toward a hill, a goldfinch flew with them. On November 1, 1944, in early afternoon a green-backed goldfinch drank at a water trough with four Mexican bluebirds.

Lanius ludovicianus Linnaeus.—At 8:30 A.M. on November 3, 1939, a loggerhead shrike, flying over a vineyard, frightened the goldfinches that foraged there. They flew into a blue oak by the vineyard, but this was also the shrike's destination, and they promptly flew onward to a group of locust trees.

Vireo gilvus (Vieillot).—At a nest just begun by a pair of goldfinches on May 23, 1939, the male in early afternoon pursued one of a pair of warbling vireos in a tree near to the nest. The goldfinch then perched and shook his wings. At 9:35 A.M. on June 1, 1939, a pair of green-backed goldfinches started to alight in the lower twigs of a pendant outer branch of a live oak about 9 feet below, and 10 feet from, a warbling vireo's nest on which the female was incubating. The male vireo chased the male goldfinch about 4 feet in an irregular course around the outer foliage of the live oak and 3 feet from the tree. The goldfinches then left and the vireo went back up into the live oak crown.

Dendroica aestiva (Gmelin).—At 9:00 A.M. on June 8, 1941, a female goldfinch flew off her nest, drove a male yellow warbler for 25 feet upstream, and then returned to the nest.

Dendroica auduboni (J. K. Townsend).—Just after a rain on January 7, 1941, three goldfinches flew to join an Audubon warbler atop a black locust. When the warbler left, the finches flew to join seven others in another tree, and these ten goldfinches flew after three more which passed by half a minute later.

Dendroica nigrescens (J. K. Townsend).—Between 5:00 and 5:45 P.M. on August 17, 1939, two goldfinches were driven away by a black-throated gray warbler which came to bathe at a small overflow stream.

Passerina amoena (Say).—At 5:30 P.M. on July 31, 1938, two green-backed goldfinches were attracted by calls of a female lazuli bunting along a creek.

Carpodacus mexicanus (P. L. S. Müller).—At 7:40 A.M. on August 17, 1942, a female goldfinch yielded her perch in the top of a blue oak to a singing house finch 3 feet away. In the morning on August 19, 1939, a goldfinch came several times with a streaked house finch to a redberry bush on the north side of a hill. It tended to perch on the more exposed and leafless twigs. Shortly after 6:00 A.M. on August 22, 1948, some goldfinches fed near house finches on a nearly bare pasture. A goldfinch pursued a house finch for about 80 yards. At 6:50 A.M. on October 24, 1944, ten males and females flew up from the open grassy south slope of a hill, in company with 35 house finches. At 6:54 A.M. on October 28, 1939, a goldfinch, 10 feet from a house finch, perched on a dried panicle of chamise and bent over to peck at foot level, apparently eating the achenes. When the house finch flew 20 yards to a small blue oak, the goldfinch followed it within 10 seconds. On November 1, 1944, in early afternoon a green-backed goldfinch drank at a water trough with four house finches.

Spinus pinus (Wilson).—At 10:00 A.M. on January 4, 1945, nine goldfinches and three pine siskins were in the crown branches of a tall leafless valley oak at the edge of a creek. Both species frequently picked at the twigs, whether eating insects, tiny new buds, or what, the observer could not tell. Individuals of both species frequently preened their feathers. An almost continuous chorus of calls was produced, but the observer could not determine whether or not the siskins called. In midmorning on January 19 four goldfinches fed at one chamise bush with three pine siskins. On January 21, 1939, a goldfinch ate nutlets from alder cones with a single pine siskin in the top of an alder beside a creek.

Pipilo maculatus Swainson.—At 7:45 A.M. on October 11, 1946, a spotted towhee flew into a coast ceanothus bush occupied by at least six goldfinches about to fly to the water tank overflow. As the towhee hopped straight through the ceanothus and toward

the water, the goldfinches hopped right and left out of its path, but they remained in the shrub and, about a minute later, took their turn at the water.

Chondestes grammacus (Say).—On November 7, 1940, a goldfinch perched on a fence with a flock of lark sparrows.

Amphispiza belli (Cassin).—On September 15, 1939, a goldfinch bathed or drank with a Bell sparrow in a small stream. Three times the goldfinch approached the sparrow even though it had previously demonstrated that it was likely to drive away the goldfinch.

Junco oreganus (J. K. Townsend).—On August 23, 1938, a pair of goldfinches was beside a creek. One was bathing near an Oregon junco. At 9:55 A.M. on September 1, 1939, a bathing junco furnished a nucleus about which six goldfinches gathered to bathe. At 9:30 A.M. on September 28, 1939, a goldfinch drank from the edge of a water trough. When a junco hopped toward the goldfinch, it hopped 6 inches away, and then flew to the opposite edge. The junco followed, but the goldfinch flew back. In the morning on October 26, 1942, goldfinches drinking at a trickling stream were chased away by a junco that came to bathe. At 11:50 A.M. on December 31, 1947, three goldfinches flew into a coffeeberry bush among some juncos there, and all flew off up a hill.

Zonotrichia leucophrys (Forster).—In the morning on October 10, 1939, two goldfinches in a group of white-crowned sparrows foraged in shade along a lane.

VOICE

In any weedy border of neglected fields small birds with yellow under parts and white patches in their wings fly off when disturbed, with a little shivering note like the jarring of a cracked piece of glass. The spring flocks gather in trees near their feeding ground and keep up a concert of twittering song. When a pair is nesting the male utters, either from an upper spray or from the air, a series of sweet twittering notes that suggest the song of a canary. The ordinary flight of a goldfinch is undulating, each stroke of the wings bearing the bird upward, and alternating with an instant of downward drop while the wings are closed. Green-backed goldfinches can always be identified by their calls. These include a plaintive *tee-yeo*, both notes on the same pitch, a *tee-ee*, the second note higher, and a single plaintive *tee*, and the jarring notes mentioned above. There is more variety in the calls of the green-backed goldfinch than in those of the willow goldfinch, and a plaintive quality which the latter lacks. Young birds, just before leaving the nest or when following their parents in early summer, utter continually a single sharp *tsi* (Hoffmann, 1927).

Florence Merriam Bailey (1923) heard soft lisping notes that green-backed goldfinches uttered in the spring. She also observed birds in undulating flight that made "gentle deprecating calls." At Glendora in southern California Joseph Grinnell on May 5, 1907, considered the green-backed goldfinches the second most voluble singers within hearing, being next to the black-headed grosbeaks.

By the first of March or a little earlier the green-backed goldfinch begins to sing. Its song is a pleasing, rapturous, canary-like burst of bird music, frequently uttered while the bird is on the wing, although this habit is by no means so characteristic of this species as of the house finch. The bird sings all spring commonly, and to a less extent throughout the summer, while even in the autumn its song is sometimes heard (Keeler, 1890). On November 1, in southern California, Frances Carter (1937) saw a female green-back perched on a cage occupied by a young male canary and a great mutual interest was exhibited.

In Arizona on April 8 Myron and Jane Swenk (1928) heard songs of green-backed goldfinches that, from its pronounced buzzing quality they thought must be that of the pine siskin, but not exactly like the siskin's song. The song was very high pitched, and entirely different from anything they had ever heard the American goldfinch utter in Nebraska, but much like that of the pine siskin. Gabrielson and Jewett (1940:548), however, thought that this bird much resembles the willow goldfinch in flight and notes. The note of the sparrow hawk is a very simple one and it has been heard rendered, on higher pitch, by an ecstatic male green-backed goldfinch (L. Miller, 1938). On March 21, 1888, van Denburgh (1899) counted seventy-two goldfinches in a large white oak. Probably there were a hundred and fifty in all, mostly *S. psaltria*, and the males were in full song, forming a charming chorus for all their lack of leadership.

Baird, Brewer, and Ridgway (1874:475) reported that

The Arkansas goldfinch was found by Mr. Ridgway among the Wahsatch Mountains, his attention being at once drawn to it by its curious notes. He first met with it in "City-Creek Cañon," near Salt Lake City, where individuals of it were frequently found mixed in with flocks of *C. pinus*. The note of this bird is remarkable for its power and very sad tone. The ordinary note is a plaintive, mellow, whistling call, impossible to describe, and so infected as to produce a very mournful effect. When the bird takes to flight, it is changed to a simple cheer, similar to the anxious notes of the male *Agelaius phoeniceus*, uttered when its nest is disturbed.

Examples of sounds by green-backed goldfinches on the Hastings Reservation: In midafternoon on February 23, 1945, four birds, two males and two females, frequently uttered single, hoarse, plaintive notes. On March 23, 1941, as a pair flew the male was in the lead and singing. On March 28, 1944, a goldfinch sang in the morning. This species had been scarce all winter, even though a few had been present continuously. At 7:30 A.M. on March 31, 1946, a goldfinch made a two-parted call something like that of a Say phoebe but with much more nasal quality. On the same day a goldfinch sang a variable song that lasted about 3 seconds. In addition there were many calls of two notes and others of single notes.

At 3:00 P.M. on April 3, 1946, a goldfinch perched about 2 feet from the top of a blue oak, facing east and giving a two-parted call. With but 3 or 4 seconds at a time for preening, the goldfinch sang steadily until 3:10 P.M. In this 10 minutes it preened itself about fifteen times. It sang a strong variable song, in addition to the two-parted note which was repeated frequently and which seems to be its most common note. In the morning of April 2, 1939, a male sang in the top of a locust tree. In late morning on April 20, 1946, a green-backed goldfinch perched on an exposed twig 30 feet up on the side of a red willow beside a creek. It perched facing south in the sun and repeatedly sang double and single notes. They sounded like: *pee-err, pee-erp, pee*. On July 12, 1938, a pair was in the vicinity of a water trough and the male was singing. In midmorning on July 19, 1939, a goldfinch sang in full song for about 3 minutes. Between 6:15 and 8:00 A.M. on July 31, 1946, calls of this species were heard from the upper parts of sycamores, willows and live oaks bordering the creek. They seemed to occur in groups of four or five birds.

At 5:38 A.M. on August 13, 1941, an adult goldfinch came to a sycamore

that held a nest, and in the next 20 minutes 111 calls were heard from the tree. At 6:58 A.M. musical chatter heard from the nest was repeated in three short bursts, the longest of which lasted about 2 seconds. The bird stretched her right wing just after finishing the notes. At 7:06 one two-parted note came from the upper part of the tree. From 7:09 to 7:18 the female was making sounds. The first was a sudden two-parted note, the first part of which was a slightly higher pitch than the second part. This was followed by an excited chatter. Both sounds were accompanied by raising the head. It seemed as if the crown feathers were raised. By 7:18, 52 notes had been uttered. Most of these were two-parted notes with the first part slightly higher pitched than the second. The notes have a wiry quality. Once, the note was reversed and the lower pitch came first. Three times the bird uttered a harsh, and lower pitched, two-parted note with the first part higher than the second. Once, it uttered a single short high-pitched note of a slightly purer quality than the most common wiry, two-parted note. At 7:32 as the female left the nest she gave four short, rapid, medium-pitched notes.

At 8:37 A.M. the female flew straight from the nest with three or four short, rapid notes that were lower in pitch than the most common two-parted note. She did not turn as on the last trip, but started in the direction of the willow and continued there until lost to sight. Before she left the nest a few harsh notes were heard. These had an upward inflection. That is, the second part was of a higher pitch than the first part of the note. In all the notes heard that morning there had been at no time any sharp break between one and another part of the two-pitched notes. With this in mind "two-parted" or "two-pitched" might be a misleading description. It is rather a slurred note starting on one pitch and ending on another, either lower or higher. At 9:50 A.M. the female from a small willow branch gave three notes, one lower and rather harsh and the other two high-pitched and smoother in quality. The latter has an upward inflection. At 10:09 a low two-parted note with an upward inflection came from the oak trees southwest of the nest-tree. The female on the nest replied with a note of the same type. At 10:09 the female started calling. At 10:11 she had called 13 times. At 10:12 she was calling again. At 10:14 the female stood up on the nest, and then slowly settled. There were ten calls between 10:12 and 10:16. At 10:25 the female stood up and lowered herself again on the nest. At 10:45 the female stood up and settled again on the nest. From then on her calls became louder and more varied. She uttered one chatter and two lower pitched calls which were harsher in tone.

At 8:24 A.M. the next morning another goldfinch called from the oaks. There was a pause of about 30 seconds before the female called. Once she started calling, the observer did not hear a response from any direction. At 8:42 the female started to call loudly, calls with a down inflection on the end. Two responses came from a bird close by. The male entered the tree from above and approached the nest by hopping down from branch to branch. While the male approached the nest the female was in a flurry of excitement. She kept emitting bursts of high-pitched chattering sounds. Only the male made any noticeable sound on the nest. He uttered one single note after the fifth time his head was thrust toward the female's head.

In early afternoon on October 22, 1944, six birds kept up a thin chatter of calls from a willow near a water trough. The observer could not see them, for they were up in the crown foliage.

At 2:00 P.M. on April 3, 1938, a male was singing in a blue oak close to a house on the Hastings Reservation. At 6:00 A.M. on May 28, 1942, a female was incubating two eggs. She gave a nasal *whee, whee, whee*, as the observer flushed her by putting his hand 8 inches from her. At 5:30 A.M. on June 6, 1940, a green-backed goldfinch flew in a circle 60 feet in diameter. It circled six times, maintaining a constant altitude of 30 feet and described a uniform circle each time. It sang all the time that it flew. On June 11, 1939, one male green-backed goldfinch perched in the nest-tree of a Lawrence goldfinch, where it called *to-hee*, a wheezy note, at intervals. At 7:34 P.M. on July 1, 1941, a sound from a green-backed goldfinch was the last recognizable call of the day. At 5:15 A.M. on July 16, 1942, there were mellow pipings from a flock near a creek. From 9:10 to 9:30 A.M. on July 21, 1948, a group of about five goldfinches kept up an almost constant chorus of musical and whistled *tchee* notes. At 9:20 A.M. on August 2, 1939, the voice was only a twitter, with no mate-calls or location-calls from the young. There were few adults, more females than males, and they rarely made sounds.

At 6:30 A.M. on August 16, 1949, fifteen, or more, green-backed goldfinches were singing, feeding, preening, and simply perching in a red willow overhanging a creek 10 feet downstream from a water trough. For 25 minutes they remained in the willow or others near by, occupied mainly by simply sitting or flitting around among the branches. No more than eleven were visible at any one time, but more could be heard singing and calling.

The song of a male goldfinch was a long disorganized series of faintly melodious notes rising and falling many times, but most often rising. Frequently interspersed throughout the long song (sometimes 30 or more seconds with only a few short breaks for a fraction of a second) were sharply rising slurred notes giving it a characteristic quality common to many finch songs. Other notes uttered by this bird were light metallic clanking sounds made frequently by the birds both perched and in flight. Another sound was a clear, plaintive descending note, slightly less than a second long. This note often is heard when the bird is in fairly dense foliage, often when the bird is alone, and less frequently when they are in their usual groups of seven to twelve.

At 5:02 on August 19, 1942, this goldfinch was the second singing bird of the morning. Two males were seen along a creek, the first ones for weeks. At 8:30 A.M. on August 26, 1949, the goldfinches seemed to be maintaining an almost continual series of musical notes involving most of the ten or fifteen birds that remained close to the area. One notable call was a pair of clear, whistled notes given in close succession, the second higher than the first. One bird was predominantly occupied in making this sound on a bare sycamore twig 30 feet above the ground. Other birds answered with a less melodic whine, usually descending, but sometimes ascending. The originator would usually inject a similar whine with the two or three answers it would get and answer within 4 seconds with the clear, two-noted call. Once it repeated this call three times at 1-second intervals; then it waited 3, 3, and 4 seconds before

repeating it. Both sexes participated in this, the most active participants were sitting in the shade flicking their tails and bodies with each note. The clear, two-noted calls elicited much less flicking than did the whine.

In the morning on September 16, 1940, several goldfinches in the top of a dead cottonwood near a creek sang continuously. At 7:05 A.M. on September 16, 1944, a flock of eight goldfinches flew over an observer. They circled and landed in a large willow in 15 seconds. All chattered away, but they did not appear to be feeding. Between 2:30 and 4:00 P.M. three different flocks, averaging about seven birds, were seen. Each bird seemed to be keeping up a steady "conversation" with its neighbor. At 6:45 A.M. on September 20, 1944, five birds in a valley oak made a loud rapid chatter, but in 15 seconds all had calmed down. At 9:00 A.M. on September 29, 1944, a flock of ten males and females was heard and seen in the very top of a 20-foot willow, hanging to small branches, swaying in the breeze, and keeping up an incessant chatter of thin whistle-like call notes. Two took flight and disappeared upstream flying with a deep undulating flight, 50 feet in the air, chattering as they went.

At 3:20 P.M. on October 4, 1944, birds chattered from tree tops near by. Several times one flew to the top of a 20-foot walnut, perched at its top, looked about, chattering as it did so, and then suddenly flitted off out of sight. Judging from the chattering there were about ten birds. At 10:55 A.M. on October 31, 1948, a flock of about twenty goldfinches was in the willows beside a creek. Several sang a squeaky, warbling song in chorus, while others made a variety of clearer notes. The observer had heard this singing occasionally since early fall. It had resemblance to some sounds of yellow-billed magpies and scrub jays.

FIELD MARKS

Half the size of junco. The sexes differ both summer and winter. Male: Body plumage dark greenish above, yellow below; whole top of head, and wings and tail, black; in flight a patch of pure white appears on middle of each wing and another shows at base of tail. Female: Dull brown, green-tinged above, and dull yellowish beneath; white patches, showing on wing and tail in flight, small or obscure. Flight course of both sexes undulating. Voice: Male has a pleasing canary-like song; both sexes have plaintive-toned call notes.

The green-backed goldfinch is slightly smaller than the Lawrence. The green-back has yellow rather than white at the under tail coverts. The white on the inner webs of the outer tail feathers of the green-backed goldfinch extends to the bases of the feathers, but not to the tips, whereas in the Lawrence goldfinch the white is confined to the middle of the feathers, reaching neither the bases nor tips. The marks on the tail are to be seen satisfactorily only when a bird is in flight. The green-backed goldfinch never shows any yellow on the wing, whereas the Lawrence goldfinch always shows this color in considerable amount. The male green-backed goldfinch is quite dark-colored above, darker than the male of the Lawrence. The female green-backed goldfinch is merely greenish, with the upper surface brown-tinged; and she lacks prominently contrasted markings of any sort (Grinnell and Storer, 1924:435)

ENEMIES

Plath (1919) made studies on nestling birds at Berkeley in the summer of 1913. In a nest of young green-backed goldfinches all the nestlings died. The observer then discovered that the birds and the nest were infested with maggots about 1.5 cm long and 0.5 cm wide. Out of the thirteen goldfinch nests examined eight were infested with these flies, *Protocalliphora azurea* (Fallen) [*Apaulina*]. The percentage of infestation was 61. The larvae attach to the nestlings and ingest blood from them. Later, they pupate in the bottom of the nest. Compact nests such as goldfinches build showed a greater infestation than nests of loose texture such as brown towhees build.

Anthony (1923) found Argentine ants (*Iridomyrmex humilis*) in Balboa Park, San Diego, California, swarming over trees and nests recently abandoned by green-backed goldfinches. He concluded that the ants had caused the desertion of the eggs. In the same area he found a small nestling goldfinch less than a week old that he thought had been taken from the nest by the Brewer blackbird that was vigorously pounding it. In Santa Clara County, California, Atkinson (1901) found two green-backed goldfinches that a loggerhead shrike had impaled on a barbed wire fence. In each instance the barb passed through the neck from side to side just at the base of the skull.

Woods (1930) found a green-backed goldfinch incubating three of its own eggs and one cowbird egg. The nest was abandoned before the eggs hatched. Peyton (1936) reported in the *Condor* the taking on July 22 of a nest with three eggs of this bird, and one egg of the brown-headed cowbird.

Green-backed goldfinches were among the birds destroyed during a fumigation of orange trees on November 25, 1911, at Covina, California (Howell, 1914).

At 3:25 P.M. on May 18, 1940, in an open field on the Reservation, two goldfinches fed on fiddleneck. Two minutes later they were frightened away by a ground squirrel which ran within about 5 feet of the birds, which flew off together, with short trills.

At 5:15 A.M. on July 15, 1938, a young green-backed goldfinch with an injured wing was at the side of a lane, apparently hurt by flying into a fence. At 9:15 A.M. on July 27, 1942, near



Fig. 8.—This immature green-backed goldfinch was dead and impaled on a 5-inch stub of canyon clarkia in July, 1942.

a creek an observer found a female goldfinch, two days dead and impaled on a 5-inch stub of canyon clarkia. The blunt tip of the stem may have been formed by grazing deer. Apparently the bird attempted to land on the grassy flat 25 feet from the creek and the stub pierced the right alar membrane. The bird was weakened by fluttering from the ground upward 2½ inches, as shown from the extent of blood on the stem, and died of exhaustion. The left remiges, particularly, showed abrasions from the struggle.

Newly hatched green-backed goldfinches were found dead under a tree after a wind storm in southern California by Edwards (1919).

BEHAVIOR IN FALL

In early August, 1939, on the Reservation goldfinches were usually paired or in small groups; evidently some families were still united. At a water tank stream flocks of young were frequently seen, but not often in the chamisal. Perhaps the adults remain paired after nesting, while the young congregate in flocks. On September 1 the goldfinches were not numerous in the morning; only two flocks were observed in half an hour and those contained less than twenty birds each. Formerly, from 50 to 100 birds were in evidence most of the time. This day was cool, cloudy, and streams might supply water elsewhere. In midafternoon on September 3 a few groups of goldfinches, only 5 to 15 in a group, came to a tank overflow in 20 minutes. None ate leaves or seeds here, nor did they remain long. The rains had removed the need to remain in the vicinity for longer periods.

At 10:00 A.M. on October 26, 1942, two green-backed goldfinches flushed from the chaparral at a water tank overflow. They flew up a canyon. Others still piped and drank at a trickling stream beneath the coast ceanothus. One sipped four times. Later they were chased away by a junco that came to bathe. Probably they bathed unnoticed as two piping goldfinches preened in the top of a bush, in shade, at 10:15 A.M. Later three flew away. None was an adult male. In October the green-backed goldfinches were infrequent, usually in the vicinity of water, and in company of Lawrence goldfinches. Groups were small, even at a tank overflow, where they were formerly numerous. Generally some were there, however. On November 18, 1942, fifteen green-backed goldfinches were in the tops of oaks at the edge of chamise at the summit of a hill. There was much singing as the clouds broke and the sun nearly broke through, but the birds became silent when the drizzle began again. There was a preponderance of males in bright plumage.

BEHAVIOR IN WINTER

At 9:45 A.M. on December 7, 1944, thirty goldfinches perched in the tops of willows and valley oaks at the edge of a creek. A chorus, almost continuous, of calls was audible, but the observer had difficulty in seeing all of the birds. During the several minutes he watched them, he saw no foraging. Aside from the few individuals occasionally hopping or flitting from one perch to another, they were sunning or preening themselves.

On December 22, 1937, the green-backed goldfinches, like the house finches, had nearly all left this place in mid-December, possibly on account of more favorable forage elsewhere, or more widely available water. At 3:45 P.M.

on an exposed slope eight or ten birds perched on tops of chamise busily eating achenes. At 11:10 A.M. on December 31, ten goldfinches perched quietly at the top of a leafless valley oak. Some preened; others perched with feathers fluffed out. At 2:30 P.M. on January 2, 1938, two were in oaks. The next day a few were in flight over a pasture. During the morning on January 3, 1945, infrequent calls were heard from occasional flights of six to ten goldfinches overhead. At 2:45 P.M. nine perched quietly at the crown of a leafless valley oak. The birds preened with feathers fluffed. At 10:00 A.M. on January 9, 1945, seven goldfinches, males and females, perched at the crown of a leafless willow at the edge of a creek. Some picked at new buds on the twigs, others preened. Calls were frequent. Suddenly, all the birds flew off up the creek, calling as they went, flying with shallow undulating flight, to join other goldfinches that called there. A few songs were heard also.

At 9:20 A.M. on January 10, 1945, a chorus of loud calls was audible as an observer walked down a lane. Goldfinches perched at the tops of near-by oaks and willows. On January 11 many goldfinches called in trees on the adjacent slope. None was seen, however. At 9:00 A.M. on January 12 several goldfinches were heard in the same area. At 9:10 A.M. on January 20, 1938, nearly half of a flock of more than 100 goldfinches ate achenes of chamise. The flock moved over the patch, every few minutes flying up to higher perches in the near-by oaks, and then flying down to the chaparral, often in a slightly different location. Sometimes eight or more were in one small bush, each perched at a cluster of fruits and eating as fast as it could. They seemed completely tolerant of others of the same and other species. At midmorning on January 27, 1945, fifteen goldfinches were perching in willows at the edge of a creek. An almost continuous chorus of audible calls came from them. Males and females were present in about equal numbers. At 10:42 A.M. on January 28, 1945, six goldfinches perched on twigs near the crown of a 40-foot blue oak at a boundary fence on a hill. They preened and uttered an almost continuous chorus of calls. Nine pine siskins were in the same tree. This morning the green-backed goldfinches and the juncos were the most numerous species to be seen. They were in the oaks and in the chamisal. On January 31, 1943, there was much chattering among green-backed goldfinches in the willows along a creek. A large flock still roosted in a live oak and another flock of fifty birds roosted in another live oak beside a creek.

In late afternoon on February 4, 1938, 200 to 300 goldfinches were in trees next to a barn. Many sang the canary-like song. Most of them were in the tops of bare valley oaks, and some fed in the outer branches of a live oak. At 10:30 A.M. on February 7, 1938, twenty-five green-backed goldfinches together with Lawrence goldfinches and pine siskins fed on chamise achenes at the bottom of a small canyon. On February 15, 1938, the sound of a squeaking branch at 30 feet away caused a flock of twenty-five goldfinches to fly to a near-by live oak where each picked a position on the top of the uppermost shoots of the flattened crown. A minute later all the birds left but two, a male and a female. They stood for half a minute, then flew in another direction, the female leading. After 4:00 P.M. on March 23, 1938, twenty-five, or more, green-backed goldfinches with a large flock of Lawrence goldfinches, juncos, lark sparrows, and house finches foraged in a vineyard.

Lawrence Goldfinch

The Lawrence goldfinch (*Spinus lawrencei* (Cassin)) is closely restricted to California, but some of the birds leave the state toward the southeast in winter. The species lives in the drier, interior parts of the state, toward the south. It is fitted to live where the seeds it eats and the water it requires may be far from the trees where it nests. Modification of nesting behavior to meet this situation involves formation and maintenance of pairs in flocks before the nesting. The male feeds the female through nest building and incubation, and in early stages of care of the young. In incubation the female remains on the nest almost continuously, and the male brings food at intervals that tend to cluster around 30, 60, and 90 minutes long. Feeding of young in the nest is at fairly uniform hourly intervals. This might be regulated by the time required to gather and prepare the food and also be influenced by hunger limits on the part of the birds to be fed.

The Lawrence goldfinch has been characterized as the most striking, although not the most abundant, goldfinch in California. My interest in the bird has been held also by the sharp limitation of its range, the irregularity of its occurrence, its affinity for hot and dry situations, the prominence of seeds of native plants in its food, its dependence on water, the permanence of the flocks, the long period through which the birds are paired, and the peculiarities in its nesting that appear to be related to these traits.

This goldfinch nests southward into Lower California from Sonoma County along the coast and from Trinity and Shasta counties interiorly. In winter some of the birds remain as far north as San Francisco and some move southeastward across Arizona as far as western New Mexico. In its summer range the bird is not common, especially northward, and its numbers in one place tend to vary considerably from year to year. Its distribution is discontinuous and the time and place of its movements are irregular. Compared with its close relatives this goldfinch lives in hotter, drier places. On the Hastings Reservation we see it in winter along with green-backed goldfinches in the chamisal and where there is water along the intermittent creeks. In spring it ranges over open ground wherever abundant small seeds are produced. In the nesting season the birds go to the hills where there are oaks, mainly live oak and blue oak.

Observations on the Reservation make me believe that the kind and amount of seeds produced each year are important in determining the number of birds present and the length of their stay. The native plants, in this instance, seem to be eaten more than others although a few introduced species have been eaten heavily. The changes in vegetation, especially the reduction in some of the weedy species with the trend toward stabilization accompanied lesser numbers of goldfinches. Search for particular kinds of seeds takes the birds to varied kinds of habitat.

The spring of 1938 was a year of abundant annual plants that produced a heavy crop of small seeds suitable for goldfinches and other finches. Throughout the season the birds fed in large numbers. In the corresponding season in 1955, the annual plants were dwarfed and had scarcely produced any seeds on the same slopes, and no goldfinches were foraging there.

For two months previous to June 22, 1949, this was the most numerous

species of goldfinch in a canyon on the Reservation. The numbers had increased as the young birds came to feed along with adults in patches of fiddleneck on the open ground. The numbers, however, were smaller than in previous years, and usually only one or two birds were seen at one time. Within a week before June 1, 1950, this species became numerous in the patches of fiddleneck. These patches were as large, or larger, than they had been in thirteen years. There were some young birds, but the impression was that most of the flocks had come from elsewhere. In 1945 a foraging flock increased greatly in numbers at a place where they fed on nutlets of fiddleneck.

Hoffmann (1927) wrote that birds are as a rule so regular in their habits that a student can find year after year a pair of birds which may have traveled a thousand miles or more to and from their winter home and yet returned to the same spot to breed. It is interesting, therefore, and puzzling to find a few birds like the Lawrence goldfinch which are more gypsy-like. A valley in southern California may be filled with the black-chinned gray-bodied birds one summer and the next year contain not one. As a rule the Lawrence goldfinch is found in hotter, drier portions of the State than either the American or green-backed goldfinches. It is a bird of the foothills or mountain valleys, particularly from Los Angeles southward.

Lawrence goldfinches occur in summer in Lower California nesting as far south as Laguna Hanson, on the Sierra Juárez (Huey, 1928:159). The same observer found the species on June 14, 1923, at La Grulla, 7200 feet, San Pedro Martir. Huey saw about 100 birds on February 25, 1925, at Rancho Las Escovas on Llano de San Quintin, near lat. 30°30'. This is the southernmost locality for the species. The birds are sometimes abundant in winter on the lower Colorado River.

The first nest of the Lawrence goldfinch in Arizona was found by Glenn Bradt at Cienega Springs, near Parker, about March 15, 1952. The young left the nest on or about April 17.

Van Rossem collected in the vicinity of Mecca at the north end of the Salton Sea from March 18 to 31, 1911. Lawrence goldfinches were nearly as common as green-backed goldfinches, but they were not yet in pairs and specimens showed no sign of breeding (1911). Lawrence goldfinches have been reported on Catalina Island in May and on Santa Cruz Island in April in different years (Howell, 1917:132).

COURTSHIP

Before incubation starts, members of a pair are more strongly attached to each other than is the case in species that are usually considered as territorial. In this goldfinch an attacked male does not leave his mate at this stage. The strong bond wanes after the start of incubation. The male is less aggressive than many other kinds of birds, and his attacks are relatively mild. However, the female is quite fierce in driving other species or members of her own species.

When the nest-building female leaves the nest on a long trip she usually utters a flight call and this appears to cause the male to follow her. On short trips there is no flight call and the male does not follow. The nest-tree is the most usual song perch for the male, but he may sing from other perches when he is in the neighborhood. Once, the pair, on arriving, stopped in a

tree 20 feet from the nest-tree. The female flew to the nest and the male remained and sang where he had perched. A minute later when a strange male settled in a tree 40 feet away, the male owner of the nest chased the intruder out with song while the female gathered material near the nest. While the female was on the nest, the male sang from the 40-foot distant tree, but later he came to the nest-tree.

In the morning of February 12, 1938, a male and female goldfinch lit in the top of a blue oak where they were joined by a Mexican bluebird that came from a mistletoe clump 5 feet away. In the next 3 minutes there were call notes from all three birds. The bluebird left and then the male goldfinch sang for 2 minutes while perched 2 feet away from the female. Next, the female flew down the canyon followed by the male. When the male came within a foot of the female, she would dive, closely followed by the male, and a moment later the two would shoot upward, the male still close behind the female. The birds flew out of sight in this manner.

Behavior of Lawrence goldfinches in part of the spring was traced under special conditions in 1938. Favorable food plants in abundance on open, cultivated ground in a small vineyard attracted a large flock of foraging fringillids—mainly Lawrence goldfinch, green-backed goldfinch, house finch, Oregon junco, and lark sparrow. From 50 to 200 Lawrence goldfinches were present daily for nearly a month, beginning in the middle of March. The largest flocks of birds foraged on a south-facing slope in the afternoon. The foraging was interrupted at intervals when the whole flock would fly off to a fence or to a near-by, isolated, blue oak. Most of the singing took place in the tree. There were indications that the goldfinches were already paired. When they rested in a tree, they usually sang facing the sun. When the male was perched, the nearest bird usually was a female. Occasionally, one or a few would perch on tops of grape stakes; once two birds perched on the same stake.

On the morning of March 17, 1949, a male sang in the treetops in a canyon for nearly half an hour. Then a female that had been in the vicinity flew to the tree and joined him. The two birds soon flew off down the canyon.

At about 9:00 A.M. on April 4 a male sang as he faced toward the east from the top of a tall, leafless sycamore in a canyon. No other goldfinch was in sight. On April 10, 1950, in a group of four goldfinches in trees, a male displayed with head and neck extended as he sang. Then all four birds flew away. Early on April 15, 1951, a pair of goldfinches perched on a valley oak limb 7 feet above the ground. The singing male was 6 inches from the female with his head extended and feathers compressed against the body. By April 24, 1946, the flocks of goldfinches were in pairs, the members of which kept close together and followed each other. One such group contained at least eight Lawrence goldfinches and one green-backed goldfinch. Mixture of the two species is commonly observed in the flocks. Singing and posturing among the goldfinches on the afternoon of April 26, 1938, was more pronounced than earlier that season. At 9:00 A.M. on April 30, 1940, at least two pairs were in a sycamore. The males kept close to the females and followed them from perch to perch.

At midmorning on May 20 an observer watched a female quivering her

wings before a male. The male took no notice, and the female kept flying up to him. Another female was in attendance the whole time, keeping close to the posturing female, and joining in when the latter pursued her mate. The intruding bird often perched a few inches from the paired female.

About 10:00 A.M. on May 22 a male fed an adult female. The birds were near a nest high in a tree. Quivering wings of the female spread less widely, and they moved less rapidly than the observer had detected in related species. At 8:30 A.M. on May 23 a flock of 15 to 20 Lawrence goldfinches with a few green-backed goldfinches flew to a low, bushy willow when disturbed. After the birds perched, they were obviously arranged by pairs. Ten or more times males flew at other males in efforts to drive them from the near vicinity of a female. This was always a Lawrence driving away another male of the same species except once when a green-backed male was driven. Usually a move of only 5 or 6 feet was required for the pursued bird to avoid another drive. Both birds would then settle on perches again.

Shortly after 7:30 A.M. on May 23, 1942, a pair fed on fiddleneck nutlets along with four green-backed goldfinches that later flew off in a group. The Lawrence goldfinches then flew to a perch 4 feet aboveground in a coffeeberry bush with the male on a twig 4 inches above and 6 inches away from the female. Next, the male flew out over the adjacent clearing, but the female did not follow. After flying about 50 feet the male returned to his original perch. About a second later he flew down to the female and, suspended by beating wings, he mounted for about a tenth of a second. The male returned to the perch, circling over the field, returned, and again mounted the female briefly. This time both birds flew away together. Coition was seen again two days later in the same area. The birds perched 2 inches apart on a fence wire 3 feet above the ground for half a minute. The male then flew up, hovered over the female, and flew out over the field. The female kept 2 feet behind the male and a little to one side as they turned and flew toward the wooded area on a hill where these birds regularly nest.

At 4:00 P.M. on May 25, 1939, the male of a pair on feeding grounds followed 3 feet behind the female. After they landed in fiddleneck and began to forage, the male was more vigilant than the female. Shortly after 7:00 A.M. on May 26 at a nest where incubation was in early stages the male fed the female and she moved from the nest to a perch 6 inches away. The male left a perch 4 feet above the nest to fly down and mount the female. Early in a late May morning a male and female flew into a large blue oak in a nesting colony. The male perched about 6 inches from the female and then flew at her. The female dodged and moved 12 inches away. The male lit 6 inches above and 2 feet away from her, and then hopped through the twigs until he was 6 inches from the female, and flew at her. The female dodged and the male landed a foot away. As the male began to approach the female again, she flew out of the tree and kept 3 feet ahead of the male.

In the morning on June 1, 1941, about twenty goldfinches perched on a fence. In a pair on the top wire the male was 20 inches from the female and he sang a low song, barely audible 10 feet away. Another female lit on the wire 15 feet away, and immediately the male changed his behavior. He became attentive and assumed a pose in which the body was slender, with neck and head extended in a line to make a thin, stiff attitude. He began

to sidle towards the newly arrived female. The original female then began to pay attention to the performance, and she flew to a perch almost directly below the intruder which then left the fence.

At 8:00 A.M. on June 3, 1938, a pair of goldfinches was in oaks in a dry gully. The male was singing and calling. The female often pursued the male which then postured and sang. The next morning at 5:45 another pair was seen in which the male followed the female. On the morning of June 7 a male and two females were together. The male sang to both females and both females postured. The females followed the male to a creek where all three drank. Later one female flew off and the male continued to sing and posture before the other female.

In early afternoon on June 7, 1939, a pair of goldfinches feeding on fiddleneck flew along a fence ahead of the observer, keeping 15 feet away. At first the male waited for the female to fly, but as the observer came on the male would fly and then the female. Another female flew over as these two birds moved ahead of the observer. She came back and alighted 1 foot from the male and on the opposite side from his mate. The male sidled toward her, and reached his bill out toward her head, but she pecked at his head and drove him away. The male flew near his mate and both flew 5 feet south of the lone female, where they began to forage. The male was not actively feeding. He watched the strange female, who presently flew away. The male then began to feed 8 inches from his mate.

In the morning on July 1 half a dozen foraging goldfinches tended to be in pairs. On July 3 a male goldfinch came in the morning to his nest several times to look about and feed the female on the nest. The female quivered her wings and opened her bill. The male perched on a small twig in front of her and put his bill in hers twelve times. When the male came to the nest on July 10, the female quivered her wings the entire time, but she became more vigorous whenever the male began his tinkle song. The male was not singing when the female finally left. He followed 3 feet behind her. In midafternoon on July 11 the adult goldfinches came to the nest accompanied by an extra female. The two females perched at the south side of the tree and one chased the other from a perch and took it herself. The male perched 12 inches above, and 10 inches away from, the nest for 15 seconds and then fed the young from the rim, and then both females joined the male at the blue oak. The second female returned to the nest at once and fed the young almost twice as long as either male or female. Then all the adults tinkled as they flew. The young were equally eager to be fed by either female. They could not differentiate.

Early in the morning on July 12 an observer heard a male call in a black oak 20 yards from the nest-tree. The female tinkled as she flew and perched at the side of the male. Both flew after 2 seconds. At 5:43 both adults arrived, the male flew to the nest-tree and the female perched at the blue oak 20 feet east. For half a minute the male perched 30 inches away and 8 inches above the nest. His single call blended two notes, as he fed the young from the rim, and then flew to the former perch, and sang for 20 seconds. He flew to the blue oak and perched 15 inches from the female, and sang. At 5:45 the male copulated with the female twice and both birds flew away. The female had been quivering her wings. In midmorning a female left her perch

almost as soon as she alighted and flew to the north side of the nest where she fed one young on the rim. When she had finished the feeding, the female flew to a twig 20 inches away from the nest where she began to quiver her wings and tail in unison, but spasmodically, while the male sang at his perch. When the male flew to the nest, the female perched 1 inch away with her bill half open, head thrown back 20°, and wings quivering. The male alternated feedings, two to each young, and then flew to a perch 30 inches away and 8 inches above the nest where he continued to sing. The male and the female left simultaneously.

Adult goldfinches flew to the nest-tree from a valley oak at 10:13 A.M. The female perched out of sight: the male perched 20 inches below and 15 inches from the nest. He gave the *ee-eu* call three times and looked about for 30 seconds. He fed the young, flew 30 inches away and 8 inches above the nest, and began to sing. The female flew to the rim and fed the young, pausing 4 seconds before flying to join the male. The male flew 20 feet to a blue oak and renewed his singing as the female approached. The female took the male's perch, cleaned her bill, and flew northward when the male tinkled. The male followed her. Both flew slowly with short undulations, and they stopped at a black oak 75 feet away where copulation took place.

In midafternoon the pair flew to the nest-tree. The female perched 10 inches from the nest for 10 seconds and then flew to a perch close to the rim of the nest. The young bird moved onto a limb in front of her. The male flew to the nest and fed the young alternately. The female moved to the rim and quivered her wings while the male fed. The male flew 30 inches from the nest and 10 inches above it. He began to sing. The female fed the young and then remained motionless at the nest except for quivering wings. The young bird kept begging until the female left at the end of one minute. She flew to the male and landed on his back. She balanced precariously and then hopped down to a branch at his side. The male flew to a blue oak and sang. The female wiped her bill on the branch and flew. When the male began tinkling, the female followed him. This tinkling by the male always seems to arouse flight in the female.

At 3:56 P.M. the adults flew to the nest-tree from a valley oak. The female perched within 10 inches of the nest. The male fed the young birds rapidly six feedings each in 8 seconds. Then he flew to a perch 30 inches away and 10 inches above the nest, and sang. The female, meanwhile, fed the young and flew to his perch. As she neared him, he again flew to the blue oak and resumed singing. The female wiped her bill on the branch. She flew when the male tinkled, and she closely followed him. Fifty feet from the nest the male caught the female and there was a short flurry before they continued their flight.

At 5:14 the adults flew to the nest-tree from the valley oak. The female perched 20 inches away from, and 3 inches below, the nest for 30 seconds before going to the rim and feeding the young. Afterward she waited 5 seconds and then perched 2 feet away before she came to a perch 7 inches above the nest. The male flew to the nest and fed the young. His movements in feeding were rapid, and he did not raise his head more than $\frac{1}{8}$ inch when changing from one young to another. Then he perched 30 inches from and 10 inches above the nest, and began to sing. The female flew to him

and alighted on his back. In the former example, at 2:51, the position of the female was reversed. She hopped down to the branch after 2 seconds and flew after another 2 seconds. The male followed 10 feet behind her.

At 5:55 A.M. on July 13 the adults flew to the nest-tree from the blue oak. The male perched 20 inches from, and 3 inches below, the nest for 15 seconds while looking about. He flew to the east side of the nest and fed the young for 3 seconds and then flew suddenly to an oak 20 feet away; the female followed to a place where the male called again. He seemed disturbed over something. The birds flew back to the nest-tree at 5:56 and the female fed the young, also from the east side. The male moved about the tree, perching at different places. When the female left the nest, she tried to alight on the male, but he flew to the blue oak 20 feet east, where he sang. The female perched 2 feet north and 1 inch above the nest and quivered her wings. The male flew back to the nest and fed the young further. Then he flew to a live oak 15 feet north and renewed his song. The female remained at the same perch and quivered her wings 2 seconds at intervals of 5 seconds. The male tinkled and the female joined him after he left the live oak.

At 6:39 A.M. the male flew to the nest-tree, perched close to the nest, and looked about. He flew to the east side of the nest in 15 seconds and fed the young. He perched near the nest and began to sing. The female flew to the nest, fed the young, and then flew to the male, alighting on top of him for 3 seconds; then the female got on a branch beside the male and both immediately flew away. At 10:53 the adults flew to the nest-tree. The male perched below the nest, called, and looked about for 1½ minutes. He sang and quivered his wings in the same manner as the female does. The female fed the young and then she flew toward the male, but she perched 3 inches above him. The male kept singing and quivering his wings at uneven intervals. The female lowered her head as if looking at her feet, keeping her head down 1 second, and then raising her head again. She repeated this at intervals of 3 seconds, looking about when the head was raised. The male flew to a blue oak 20 feet away and continued singing. The female kept on bowing her head and quivering her wings occasionally. She flew to the blue oak at 10:59 and kept up the bowing. The male quivered his wings and sang.

At 11:02 A.M. the male flew to the nest, fed the young, and then flew back to the blue oak where he renewed his singing. The male tinkled and the female left the perch with the male closely following. There was an attempted copulation on the wing. It took 1 second and the pair then flew eastward.

At 1:48 P.M. the adults came to the nest-tree from the southwest. The male perched 10 inches east of, and 8 inches above, the nest for 15 seconds and looked about. The female perched 4 feet away and 5 feet above the nest. The male fed the young and then perched 3 feet from, and 6 inches above, the nest where he sang. The female flew to the nest and fed the young. When the female was through feeding, she flew to the male and alighted on him. She remained 1 second and then moved to a branch and the male flew to the blue oak 20 feet east and sang. The female cleaned her bill on the branch twice and then flew northward. When the male tinkled for 2 seconds, he left the blue oak at nearly the same time because they flew side by side when they met.

At 3:05 P.M. the male flew to the nest and immediately fed the young. The female fed the young from the north rim 15 seconds later and then perched 20 inches north of the nest. The female bowed frequently and quivered her wings seven times in the next 4 minutes. The male flew back to the nest-tree and paused at the rim of the nest, but he did not feed the young. He then perched 2 inches to the right of the female. He sang again for 5 seconds and then both flew. There was no tinkle in flight, but it preceded the departure of the female.

At 5:30 A.M. on July 14 the adults flew to the nest. The male immediately fed the young; then flying 30 inches from, and 10 inches above, the nest, he perched and sang. The female had been perched 10 inches from, and 6 inches above, the nest, but she moved to the nest 2 seconds after the male left, and then she fed the young. Next, the female flew to the male and alighted on him. He leaned forward and she leaned backward. They remained in these positions for 3 seconds and then the female perched at the left side of the male for 2 seconds. Both flew, tinkling, to the southeast. At 6:11 the male perched 30 inches from the nest and 10 inches above it. He began to sing. The female remained at the nest for 5 seconds longer and then flew to the male and alighted on the back of his neck. She slipped off with frantic wing-beating to maintain a balance, and perched on a branch while the male flew to an oak 20 feet away and sang. The female flew when he tinkled and the male followed closely. At 8:18 the male fed the young and then went to the perch used previously where he sang. He tinkled and followed the female. The male caught the female 45 feet from the tree and there was a short flurry and one feather dropped. They continued on their way.

At 12:46 P.M. the adults flew to the nest-tree. The female perched about 12 inches from the nest and the male perched about 5 feet from the nest for 15 seconds. The male then flew to the nest and fed the young. He flew to a branch 28 inches away and 9 inches above the nest, and began to sing. The female waited 10 seconds and then flew to the nest and fed the young. She flew to the male and tried to alight on him, but he flew to the oak 20 feet away and renewed his singing. The female wiped her bill on a branch and then looked about and bowed five or six times. The male tinkled and the female flew east as the male met her and flew at her side, 6 inches from her wing tips. At 5:23 the adults flew to a black oak 25 yards north northeast and perched, calling. The female bowed her head 4 seconds and quivered her wings between bows. At 5:25 the female rose first and flew northward followed by the male.

There is close cooperation between the two adults in nesting; the male feeds the female during incubation and early brooding and then both adults feed the young during the later nesting period.

An example of behavior, possibly courtship out of season, was recorded at midday on October 14, 1939. A female delivered a continuous series of squealing notes while pushing her bill against the bill of a male. The latter retreated 8 inches. This may have been a young bird.

On July 16, 1940, a male beside a creek was closely followed by a food-begging bird, apparently an adult female.

Male intolerance.—Male intolerance of the near presence of other male goldfinches is prominent in the early stages of nesting. The examples given here show that this trait is not restricted to the vicinity of the nest, but the antagonism is directed mainly to other members of the species. In the early afternoon, on April 16, 1938, several fights were observed among Lawrence goldfinches. The activity was accompanied by song and display and usually it was between males, but this behavior seemed less far advanced than in the green-backed goldfinches at that time.

On May 22 a fight between two males took place. The birds rose facing each other for about 6 feet above a live oak, clawed at each other, and parted. A pair feeding on fiddleneck was joined by another pair. All four birds flew into a coffeeberry bush and the males began to fight. They flew out of the bush into the air when they hovered a few seconds 6 inches apart, feet drawn up as if to strike, and facing each other. The females did not join in the battle. All the birds resumed feeding, but a male once threatened the other and drove him about a foot away.

At a nest watched in early morning on May 26, in early incubation, there was much fluttering in a tree 20 feet from the nest. A male pursued another 6 inches ahead. They made a downward loop; then the pursued one moved through the nest-tree and flew northward out of sight 100 feet away. The pursuer returned to the starting place and remained there. Early the next morning two males flew into a tree 50 feet from this nest. One flew toward the other from a perch 2 feet away, and that one came to meet the aggressor. Their wings hit in midair, but the observer saw no use of the claws. The birds flew about 20 feet farther, and the pursuer caught up with and struck with its wings at the pursued one. The latter flew on, but the aggressor stopped and flew out of sight in the opposite direction. There was no singing after the victory.

Another conflict between two males took place in midafternoon when they flew into a live oak 60 feet from the nest. After they perched one pursued the other, but he stayed 3 feet behind it. Forty-five minutes later in the same vicinity two males flew into the top of a blue oak about 15 feet from the nest-tree. One flew at the other which remained on his perch and struck back. Then, after 2 seconds of watching each other, they flew about 6 inches apart and began another fight. They used their wings mostly, but also they pecked with their bills. After the second skirmish, they separated by a foot, and one moved up to within 6 inches of the other. That one did not move, but merely watched. The first one again pounced and each struck at the other in midair. Then one flew away 12 inches ahead of the other. They went through a tree and out of sight. The whole battle had lasted about 2 minutes.

At the end of May two males and a female in the vicinity of a feeding area flew to a valley oak. One male perched about 2 feet from the female, the other 5 feet away. The nearer one flew at the other, drove him out of the tree, and returned. He perched 3 feet from the female and ruffled his feathers. The fleeing male had gone to a coffeeberry bush 60 feet away. The female flew to that bush, followed within 3 feet by her mate. The female landed 3 feet from the male already there, and her mate perched one foot from the male he had pursued. He next flew at that bird and both

fluttered about in the bush, 8 inches apart, for a second and then they remained in the bush. The sounds of the fight attracted goldfinches feeding near by, both this species and the green-backed one, and several other birds flew up into the tree.

At 8:30 A.M. on June 4, 1940, three or four goldfinches foraged on fiddle-neck. When a strange male approached a feeding pair, the female appeared to pay no attention, but the male immediately postured by elongating his body, raising the tail slightly, and facing the intruder. At the same time he noticeably increased the intensity of his singing—evidently in an effort to drive away the strange male without a charge.

On June 1, 1939, two males and a female flew into a coffeeberry bush. One male landed above the other, flew down toward the lower one, and replaced him on the perch. The female flew down at the first male and replaced him on the perch. The female moved to the bush taken by the second male. In the bush the two males engaged in a fight, but without a clear victory. All three birds remained in the same thicket. At 7:50 A.M. on July 16, 1938, a male goldfinch pursued another. After both lit 2 feet apart on a fence, there was no further sign of belligerence. In midmorning on August 16, 1948, in a small group, two birds pursued each other with rapid turns and twists 3 or 4 feet above the grass. They went into low willows. In a midmorning of early October a group of six goldfinches flew from a fence to the ground to forage among green grasses. As two foraged side by side, one pecked once at the side of the other which then hopped 2 inches away.

Male and female intolerance.—In early stages of nesting, pairs of Lawrence goldfinches exhibit intolerance toward green-backed goldfinches in comparable stages of nesting. In the morning of April 20, 1939, a pair of Lawrence goldfinches came into a tree in which a pair of green-backed goldfinches was building. The female of the latter species fought with the intruding female for a long time in an attempt to drive her from the tree. Neither male was concerned with, or entered into, the conflict.

On the third morning of watching at a nest where incubation was in process, a male green-backed goldfinch called in the top of the nest tree, and then a minute later he flew away unmolested. He returned shortly to a perch 8 inches from the nest. The male of the nesting pair flew at the intruder from a live oak 15 feet south of the nest. The birds flew about 20 feet where the Lawrence goldfinch again flew at the green-backed male. They met in midair, but the intruder gave way and flew off, pursued by the owner. The female green-backed goldfinch had been a spectator about 4 feet from the battle. She followed the two males as they flew away.

NESTS

The nests of Lawrence goldfinches according to Dawson (1923:200)

are exquisite creations, highly varied in construction and sometimes quite picturesque. A dainty cup before me, an inch and a half in diameter and one in depth, is compacted of wool, flower-heads, fairy grasses, horsehair, and feathers. Another, of coarser construction, boasts several additional ingredients, but dispenses with horsehair in favor of sheer feathers for lining. A third displays a garland of protruding and highly nutant grass-heads, as chic

as a Parisian bonnet. The female, naturally, disputes the intruder's claim to such a piece of handiwork; but she does not often have to be lifted from the nest.

Baird, Brewer, and Ridgway (1874:479) wrote that

three nests of this species obtained at Monterey, Cal., by Dr. Canfield, all exhibit more or less variations as to material and style of make. They are all more or less felted, and beautifully wrought, fully equal in artistic skill to the nests of the Goldfinch. They are about one and a half inches in height and three in diameter, and the cavity is an inch in depth and one and three quarters in diameter. The walls of these nests are soft, warm, and thick, composed of wool, both vegetable and animal, fine stems of grasses, down, feathers, and other materials, all closely matted together, and lined with the long hair of the larger animals. One of these nests is made up entirely of the finer grasses, strongly matted together.

The following brief descriptions of nests and their surroundings on the Hastings Reservation characterize the nesting habitat for that area. The birds show a special choice for nesting in the lichen-festooned blue oaks of small size that grow close together on dry slopes of hills.

Near noon on April 17, 1939, an observer heard a commotion among Lawrence goldfinches in live oaks. A male fed his mate. After he had gone the female remained on the nest that was on a nearly horizontal limb 25 feet above the ground and partly screened on the southeast side of the tree. On May 26 a goldfinch nest was found on the south side of a blue oak next to the trunk and 20 feet up. It was composed mostly of lichen (*Ramalina reticulata*) on the outside and it was watched daily from May 26 to June 11.

On June 5, 1938, a nest was discovered 6½ feet up in a lower, lichen-covered limb of a blue oak on a ridge near the top of a hill. The female flushed when the observer walked directly beneath the nest in early morning and when he came within 15 feet of it two hours later. The nest was small, but rather coarsely built of plant stems and lined with whitish material. It contained four white eggs. Both adults were near by and they protested at the man's presence. Several other pairs were in the vicinity. None was seen

TABLE 1.—Time of nest building of Lawrence goldfinches

Sacramento	June 15, 1921	(Wanzer)
3 mi. N General Grant Park	June 3, 1931	(Wanzer)
Sacramento	April 1 to 10, 1950	(Wanzer)
34 mi. NW Colton, 5,000 ft.	June 17, 1934	(W. C. Hanna)
San Jose	May 11, 1929	(E. Smith)
San Jose	June 7, 1929	(E. Smith)
San Jose	June 13, 1930	(E. Smith)
San Jose	April 7, 1939	(E. Smith)
San Jose	April 11, 1941	(E. Smith)
San Jose	April 15, 1941	(E. Smith)
San Jose	April 17, 1941	(M. F. Vessel)
San Jose	May 15, 1941	(E. Smith)
San Jose	April 22, 1942	(E. Smith)
San Jose	May 14, 1942	(E. Smith)
San Jose	Mar. 31, 1943	(E. Smith)
San Jose	April 1, 1943	(E. Smith)
San Jose	April 3, 1945	(E. Smith)
Point Lobos	April 18, 1935	(J. Grinnell)
Carmel	Mar. 25, 1943	(L. Williams)
Los Gatos	Mar. 12, 1948	(E. Smith)

going to nests, but another nest, new and empty, was found 100 yards away, 2 feet up in a mistletoe clump in a blue oak. On June 6 a nest was found in a sycamore. On June 7 a female incubated on a nest on a hill. The nest was $7\frac{1}{2}$ feet up in a mass of lichen on a lower limb on the southeast side of a large blue oak. The female was near by, but the presence of a man prevented her from going on the nest. She flew to the nest two or three times. The tree was surrounded by small blue oaks and live oaks. The nest was lined with brown material, and it contained two eggs. On June 22, 1939, a nest 20 feet aboveground in a blue oak was on a limb at a 50° angle above horizontal, at the junction of a smaller branch, with a leaf cluster above it. The nest was on a northwest facing slope. The branch swayed in the wind. On July 2 a female was on a nest on the more horizontal of two branches forming a vertical crotch on the north side of a blue oak 40 feet from the bottom of a ravine.

In Coachella Valley barely above sea level Hanna (MS) found the earliest nest on April 1 and his latest nesting date was June 27 at over 5,000 feet, in San Bernardino County. The highest location was at 6,000 feet in Slover Canyon. The nest was 40 feet up and out 10 feet on a limb of yellow pine. He has found nests only 3 feet above the ground and as high as 40 feet up, with the average about 15 feet from the ground.

Robertson (1931:38), in Buena Park, reported that Lawrence goldfinches built their nests at moderate elevations in the thick foliage of the trees.

The following nesting materials were reported by W. C. Hanna (MS) as making up fifteen nests examined by him in San Bernardino County: 1) Fine fresh flower stalks; lined with cotton, *Filago depressa*, and feathers; 2) Fresh flower stems, buds and flowers; lined with feathers and short white hairs—compact; 3) Fresh flower stems, buds and flowers; lined with feathers; 4) Flower stems and leaves; lined with plant fiber, feathers and hair; 5) Small flower stems and flowers and much wild buckwheat blossoms and feathers; 6) Very fine flower stalks; lined with feathers; 7) Fine fresh flower stalks and stems; lined with fine, matted fiber and few feathers; 8) Short, fresh weed stalks, flower blossoms; lined with feathers; 9) Fine fresh flower stalks, and flower blossoms; lined with fine plant fibers and cotton; 10) Fine fresh flower stalks and cotton; lined with cotton and a few feathers; 11) Fine loose fresh flower stalks; lined with fine bark strips and a few small feathers; 12) Fine weed stems and flower stalks; lined with fine, light-colored cotton and hair; 13) Fine flower stalks and cotton; lined with cotton, *Filago depressa*, and two feathers; 14) Fine flower stalks and cotton; lined with cotton and a few feathers; 15) Fine fresh flower stalks, and flower blossoms; lined with fine plant fibers and cotton.

Colonial nesting.—Dawson (1923:199) reported that these birds colonize to some extent in isolated clusters, or in hedges, of the Monterey cypress, and he found as many as ten nests at once in two adjoining trees. He indicated that there is no flock impulse in the matter, however, for along with incompletely nests were others containing eggs, and others still with young. Mr. Wm. Twisselman has told me that he knew of colonial nesting of this goldfinch in a short hedge of cypress that formerly lined a road south of Salinas.

Wilson C. Hanna (MS) has usually found these birds in single pairs at nesting time in San Bernardino County, but in 1943 he found them to be abundant in a small area on the Mohave Desert. There were possibly a dozen nests in one small juniper, a few in two other junipers a few feet away, and still others in sage (*Artemisia tridentata*). The site was occupied by a

TABLE 2.—Nest dimensions (in inches) for Lawrence goldfinch.
Measurements provided by Mr. W. C. Hanna.

	Diameter		Depth	
	Outside	Inside	Outside	Inside
Apr 1, 1928	3.50	1.60	2.00	0.80
25, 1920	2.90	1.50	2.00	1.10
22, 1937	2.75	1.80	2.00	0.80
May 9, 1943	3.50	1.70	2.00	1.00
13, 1920	3.00	1.60	2.00	1.20
9, 1919	2.75	1.75	1.75	1.00
15, 1943	2.85	1.70	1.75	1.25
15, 1943	2.75	1.70	1.75	1.30
23, 1943	3.00	1.50	2.70	1.20
23, 1943	3.50	1.50	2.75	1.20
Jun. 21, 1936	2.80	1.50	1.60	1.10
27, 1934	3.20	1.80	3.00	1.10
16, 1918	2.75	1.75	1.75	1.10

stand of Joshua trees. The colony was at least half a mile from any water. Several of the nests were destroyed from some unknown cause.

Sharp (1907) reported this finch as common at Escondido where it nested in colonies of a few pairs in the orchards and other suitable places, with one brood only as a rule in the season April 12 to May 25. In 1906 the species was more plentiful than he had ever seen it.

On the Hastings Reservation Lawrence goldfinches tend to nest in small colonies on the slopes of a hill where there are stands of small blue oaks, especially the ones covered with lichens. The sites occupied for nesting are on the higher parts of the hill and they are about half a mile from the best food producing areas on flats along a creek or on open ground on the hilltop.

NEST-BUILDING

Behavior of Lawrence goldfinches on the Hastings Reservation at an early stage of nest building was watched at midmorning on May 14, 1938. At first two pairs were together in a rose thicket near a creek, and then all the birds were in the air, fighting. Next, one pair flew away, the female of the remaining pair pulled off lichens and other material from a rose stem, and both birds flew into a live oak overhead. The male flew out repeatedly in circles about 50 feet in diameter and returned to a site about 35 feet aboveground near the end of the live oak and almost directly over the creek. Later, a female was here several times arranging material in a nest barely begun. More than two goldfinches were in the tree most of the time, and it was impossible to be sure that all of the behavior pertained to the same pair. There were other pairs in the vicinity, mostly in the large oaks, in which the male was closely following the female or was driving away other males and singing.

Males accompany females in search of nest-building material. On the morning of May 16, 1938, a pair of goldfinches was nest building at a site 18 inches below the top of a small live oak that also contained the nest of an Anna hummingbird. The female carried material about 50 feet from live oaks, and the singing male followed her closely. Several other pairs were in the

vicinity, and there was much singing. By noon the nest was about half completed, and the birds still made frequent trips to it.

In midmorning on May 20 a female brought feathers and placed them as lining for the nest; previously only plant material had been brought. Eight minutes later the pair returned, but left to chase another goldfinch in a near-by tree. Twenty minutes after the feathers were added, there was a copulation after which the birds remained on the nest-tree for 3 minutes. Then the female left, followed by the male; both settled in a tree 50 feet away, and the male sang before they departed.

On the morning of June 14, 1940, a pair of goldfinches was nest-building 20 feet up in the upper part of a blue oak. The female gathered spider web from the lower limbs of a live oak and made two trips, closely accompanied by the male. Later trips were interrupted by the presence of a man 50 feet away. About 8:00 A.M. in mid-June a female picked horsehairs from the ground close to a saltlick. A male foraged 3 feet away, and 5 minutes later both birds flew out of sight among oak trees.

Before noon of the first day in a tree close to the nest-tree a goldfinch sang, and then the male fed the adult female, the latter with quivering wings. The pair twittered together, but there was no further excitement. Two minutes later the pair returned to the nest. Half an hour earlier similar feeding in another pair had taken place in the same tree. The next morning at 6:41 the pair came to the nest. The female called and fluttered her wings slightly. The male approached and the female repeated the wing fluttering definitely and more excitedly. The male came above her and fed her three times.

In midafternoon on June 17, 1940, a pair was on the bare ground close to a building in a canyon. The female gathered numerous fine straws. Both birds flew up to limbs of a valley oak and then off southward to a wooded hill. In less than a minute they were back. The male closely followed the female.

Two successive mornings, May 19 and 20, 1939, were spent at one nest in the building stage. The site was in a slender 35-foot blue oak on a steep east-facing slope and 20 feet aboveground. The nest was supported by small twigs, and it was partly exposed. Building was by the female only, but the male was nearly always close by. The birds of the pair were markedly aware of each other. The male sang while the female built, and he nearly always followed her when she left the nest-tree. He did not go when she collected the material from near-by trees. The observer concluded that the male knew where the female was going. The male appeared distressed when the female was not close by. The trips were in a different direction each time. Much of the material brought was lichen (*Ramalina reticulata*) that the female picked from branches of trees. Sometimes she got it from a part of the nest-tree. Once she took a piece directly above her head when she was on the nest and then carried it around in the tree and back again. She repeated this twice with much shorter flights.

On the second morning the female brought only small objects, but she spent much time working around the nest and pressing her body against the sides. Once she worked at the nest for 5 minutes and then came out on a branch. Half an hour later she was collecting material from trees, 10 to 15

yards from the nest, and she returned quickly at 3-minute intervals. At 9:30 A.M. the female brought feathers to the nest; previously she had always brought plant material. Later, when she went to a tree only 20 feet away to collect nest material, the male never left the nest-tree, evidently realizing that she was not flying far. For 10 minutes she collected material from neighboring trees and several times the male remained in the nest-tree. Then at 10:27 the female gave the usual flight call as she left and the male followed. Her visits to near-by trees when the male did not follow were not preceded by the flight call. This must be the signal that causes the male to follow the female in flights from the nest. In an example the female left the nest, twittered twice, was answered by the male; then the female flew off twittering, and the male followed.

In the last days of nest building the male sang mainly while the female worked. He sang in flight when following the female, but more persistently when perched near her at the nest. On the first morning the song was spontaneous, and not in answer to any other male. It was delivered from many branches in the tree, but not from others. Once, close to 11:30 A.M., a strange male followed the pair back to the nest. He settled and sang within 3 feet of the nest, but the male from the nest paid no attention to the intruder even though he was only 6 feet away.

The next morning, after the male fed the female three times, he went to the nest and sang quietly. The female went to the nest and the male sang close by. Then the male suddenly left the nest-tree and flew, singing, to a bush 12 yards off. He chased another male from there and then drove him from another perch. The first male returned and sang loudly in the tree next to the nest. He then sang in flight to a tree 10 yards in another direction and twice chased off a male that had settled there, singing at the same time. This male had made two flights to separate trees to chase males from the vicinity of the nest, and had left his mate to do so. The chases were mild compared to those of some other species, but the results were alike. The male had enlarged the space from which he attempted to drive out strange males.

On these two mornings in numerous instances a member of the pair drove off a strange goldfinch. The male was quick to chase other males. The female pursued other females and sometimes strange males. At least twice a male green-backed goldfinch came into the nest-tree, and neither member of the pair took notice of it. Sometimes the male flew off and there was a pursuit that could not be traced clearly. Such a flight might involve the four birds of two pairs, but usually it was mild and one bird or pair would leave. Sometimes another pair would be in the near vicinity of the nest for some time (once for 5 minutes) without the owners detecting them. Once a juvenile remained for 10 minutes 30 feet from the nest. When a strange male settled and sang within 3 feet of the nest and then came up to the nest at 11:32 A.M., the male owner paid no attention, but the female chased him away quite vigorously, with her presumed mate following, for at least 35 feet.

At 6:00 A.M. on the second morning a strange female settled in the tree. When the male went to her, she extended her head and gave a feeble, harsh call which drove him off. Then a strange male flew into the tree and at once there was an indeterminate chase between the two pairs. Another time the nest pair followed a strange pair into the tree, and the strange female drove

off the female owner. The two males perched 9 inches apart without antagonism.

The flocking habit of this species is so strong that the late nest-building pair was regularly followed to the nest by one or more goldfinches, usually of the same species, but sometimes a green-backed. After the birds arrived there would usually be some attempt to drive out the strangers, but these pursuits tended to be mild and not to extend far. Evidently the tendency to join other individuals in a flock and to follow others in flight prevented the establishment of a rigid habit of isolation for the nesting pair and the exclusion of other members of the species or even of competing members of the same sex.

EGGS

The eggs are always white and without markings. The weight per egg is between 0.82 and 1.25 grams. Fifteen sets ranged from 3 to 5 eggs per set and averaged 4.07 eggs (Hanna, MS).

INCUBATION

At 6:14 A.M. on May 23, 1939, at intervals there were faint calls from the incubating female on a nest. At 6:15 a male and a female arrived in the tree; the male twittered like the beginning of his song. His actions and the direct flight to the tree indicated he was the owner of the nest. The nest female promptly left the nest and drove away the extra female. The male followed, and all three birds disappeared. A minute and a half later the pair returned to the tree, and the female placed a head of grass in the nest. The male sang in the nest-tree for a few seconds and then sang from trees 20 to 30 yards away. Once he drove away another bird, and he circled around the nest-tree, singing, before he left. In this time the female on the nest sang, and then she became silent.

Fifteen minutes later two males and a female arrived in the nest-tree where the female was incubating. The male owner of the nest chased the other male mildly round and round the tree; the second male would not leave, presumably because his own female was still in the tree collecting nest material. As the strange female hopped into view of the nest, the nest female left and vigorously drove her off. There was no question but that male attacked male and female attacked female in this encounter. The sitting female could see the strange male as he was chased round and round the tree, but she did not leave the nest to attack him.

The strange pair moved off 20 yards, the nest female came back to her

TABLE 3.—Lawrence Goldfinch nests with eggs in California

Soap Lake	Mar. 25, 1932	(Unglisch)
3 mi. W. Gilroy	Apr. 26, 1927	(Unglisch)
Coyote Creek	May 16, 1936	(Wool)
Monument Peak	June 6, 1936	(Wool)
Arroyo Mochi	Apr. 20, 1941	(Bolander)
Fresno area	Apr. 11, 1906	(Tyler)
Claremont	July 5, 1903	(W. M. Pierce)
Los Angeles Co.	Apr. 3, 1908	(D. I. Shepardson)
Los Angeles	Apr. 23, 1892	(G. F. Morcom)

nest, and the male to the nest-tree. A minute later the strange pair again invaded the nest-tree, and again male drove off male and female drove off female. The nest female then went back to her eggs. The nest male went toward the nest; a few inches away from it he encountered the strange female again, there seemed to be a brief encounter, and the strange female left. The male did not attempt to follow her. He went to the nest, fed his female by regurgitation, and then left.

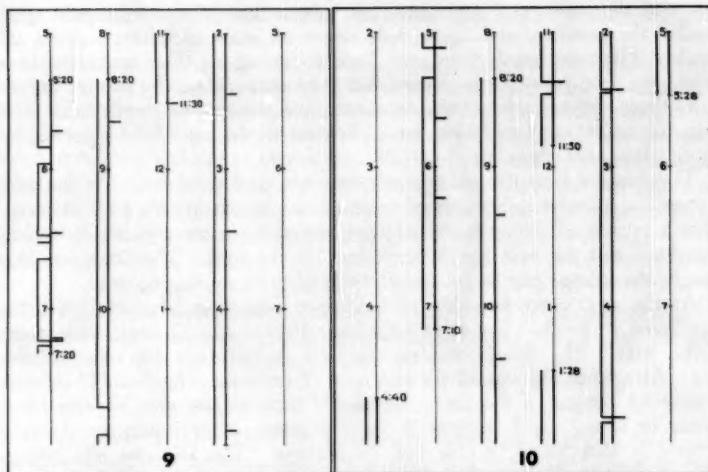
Ten minutes later the strange pair returned, and the female left her nest to chase the intruders. She seemed to attack the female and the male followed. After a pursuit of 25 yards the stranger settled for a short pause; they then moved off and the nest female went back to the nest. The attraction that brought the strange pair so persistently seemed to be nesting material.

At the nest where watching of incubation began on May 26, 1939, the eggs failed to hatch. On seven days, up to June 11, 56 hours were spent at this nest. The female was on the nest continuously for most of this time. Altogether, she was off the nest only 27 times for a total of 117 minutes or only 3.3 percent of the time. Of the 27 trips off the nest 10 were for 1 minute or less, 7 for 2 minutes, 1 for 3 minutes, 2 for 5 minutes, 3 for 6 minutes, 1 each for 7, 9, 13, and 33 minutes. The last one was late in the period when the attraction for the nest was being lost. All but two of the trips were for less than 10 minutes. Sixteen of these trips were made in early morning, before 7:15. Two were between 9:00 and 10:00 A.M. and three between 11:00 A.M. and noon. Six were made in the afternoon between 2:00 and 6:00 P.M., with half of these between 4 and 5 o'clock.

The male made 57 trips to the nest, an average of one per hour. The largest number on one day was 11 in 10 hours. Complete intervals away from the nest numbered 37. The shortest was 3 minutes long and the longest 144 minutes. These intervals showed a clear tendency to be 30, 60, or 90 minutes long. For these lengths \pm 10 minutes there were 11, 12, and 6 intervals, a total of 29, or 68 percent of all the intervals.

Behavior of female on nest.—In early stages of incubation at one nest where the female remained on the nest almost continuously, there was little variety in her activity. Between feedings by the male the exceptions to sitting quietly included the following examples. At 6:45 A.M. the female preened on the nest, working over the left side of the neck as high as she could reach with her bill. Ten minutes later she listened intently to the chipping of a male 40 feet to the southwest, but she paid no attention to the singing of a male 20 feet north. At 7:20 the female was quiet on the nest, turning her head from side to side but not looking behind her. An hour later she rearranged a piece of lichen on the rim of the nest. About 10:00 A.M. the female appeared to be asleep with eyes closed; her head was drawn down, but it was not turned back under a wing. Ten minutes later she was restless on the nest, picking at the rim and preening her neck. For the next 10 minutes she was preening constantly.

Early in the afternoon the incubating female was on the nest with her back toward the sun. She preened herself frequently, and once scratched her head. She was not quiet on the nest, but she ruffled her feathers and resettled them. After being fed she turned around in the nest and settled herself, but in about 2 minutes she turned back, stood up, and peered down into the nest.



Figs. 9, 10.—Periods on nest by female Lawrence goldfinch in incubation. On right of the columns are indicated eight trips to nest by the male. 9. May 26, 1939. Observation from 5:20 to 7:20, 8:20 to 11:30 A.M. and 2:00 to 5:00 P.M. 10. June 2, 1939. Observation from 4:40 to 7:10, 8:20 to 11:50 A.M. and 1:28 to 5:28 P.M.

She remained standing for about 10 minutes with wings half raised. She finally resettled herself on the eggs after pecking twice at something on the bottom of the nest. She swung her shoulders from side to side and worked her legs.

A strange female that had foraged in the vicinity of a nest flew into the nest-tree and perched a foot above the nest. The female on the nest froze and watched the intruder intently. The strange female wiped her bill about six times on a twig and then flew off toward other nests about 75 feet away. The female on the nest then relaxed and resettled on the eggs.

Shortly after 3:00 P.M. the female sang from the nest. There were three trills, the last one longer than the other two. There was no male in sight and none was singing. She was preening herself most of the time, but she did not scratch very often. After a feeding she settled in the nest and preened under a wing and at the base of the tail, bending almost double while resting on the nest, but she did not stand up. Then she faced northwest toward the sun. About 4:40 the female began to utter a location note, *meow*, and when the male came to the site 15 minutes later she stopped calling. After the feeding, the female settled on the nest, preened, and became quiet. In 3 hours the female had been on the nest continuously, but not quietly. There had been three feedings by the male.

On the eighth day of watching at a nest in stage of incubation, when the air became warm in the morning, the female on the nest became restless. She stood up to inspect the contents of the nest or its lining. Then she settled again. The temperature at 8:30 A.M. was 80° F. The female was on the nest

facing the west with the sun behind her. She was in a high, or standing, position part of the time breathing with the bill open. A few minutes later she was standing in the nest with wings raised $\frac{1}{4}$ inch from her sides. Half an hour later she stretched the right wing and then settled in the nest. She moved about, constantly preening, mostly on the breast. An hour after this session of watching started, the female turned to face the south and began vigorous preening. This included scratching the head on both sides, stretching wings, ruffling and shaking the feathers, standing up in the nest, and finally preening the breast. This whole performance on the nest lasted about 5 minutes.

In the afternoon the female on the nest had her head in the sun and her eyes open. She stood up in the nest occasionally, but she was not so restless as in the morning, and she did not preen so much. Most of the preening involved the tail base as though she was getting secretion from the preen gland.

Twice the female called the ringing call and then the querulous *mew*. Then she continued the first note at intervals of 4 seconds, for 5 minutes. Between calls the bird preened. Because it had been 75 minutes since the last feeding, it seemed likely that the calls were to attract the male. Finally she remained silent and preened occasionally. The male fed her at 4:50 P.M. after 144 minutes. She then left the nest for 2 minutes.

During most of the days when incubation was watched, in early stages, the female left the nest only for short intervals, and then only just after she was fed by the male. On the fifteenth day the female did not strictly follow this program, and she left the nest on four occasions when the male had not come to the nest. Behavior of the male on his trips to the nest showed that he usually tried to coax the female to leave.

In the nest when incubation was prolonged because of failure of the eggs to hatch, the program was still being followed on the seventeenth day. Early in the morning the female was quiet on the nest, but at 5:40 A.M., about 5 minutes after sunshine hit the nest, she began to preen. The warmth of the sun may have caused the preening.

Shortly after 6:00 A.M. the male arrived in company of a second male which continued on in flight. The mate went to the nest and approached by a route used earlier. The female began to quiver as soon as the male reached the beginning of the customary route and possibly because she could see him there. After the male fed her, he waited only about 5 seconds before he flew off out of sight. The female then began the mate call which she uttered at varying intervals for about 10 minutes after the male had gone.

Twenty minutes later the male came alone and went to the nest by a shorter route than the one used earlier. He fed the female, hopped out to the end of the approach twig, and then returned to feed her a second time. Usually there had been only one feeding at each trip. The male then waited for the female, calling a short *whit* to her, which she answered; but the female did not leave. After the male flew away, the female began to utter the mate call and a whistling note.

Female off nest.—The incubating female goldfinch remains on the nest almost continuously except for short intervals when the male waits for her

to leave after a feeding. At a nest where the eggs failed to hatch, the female was still incubating on the 15th day after watching started. On that morning she left the nest twice. First, at 5:14 she went off without the male coming to the nest. She joined him 10 feet away and both birds flew out of sight. Both birds returned after 6 minutes, from another direction, the female ahead of the male. He perched 2 feet from her. The female returned to the nest after standing on the rim to inspect it. The male came to the nest, but he paused only to look in and then moved away.

A little more than an hour later the female accompanied the male away after a feeding. They were back after 1 minute and she went onto the nest. After another 4 minutes she flew off when the male was not present. She was gone for 7 minutes and then went back onto the nest after poking her head into it for about a second. This behavior showed that the regular program of incubation was beginning to change.

Another of these spontaneous trips away from the nest by the female occurred in the late afternoon. In her absence the behavior of the male demonstrated numerous characteristics of the automatic nature of his behavior at the nest during incubation. By 5:02 the female had been on the nest continuously for more than 3 hours (216 minutes). The male had been to the nest briefly three times. At that time, after more than 5 minutes of peering about, preening, ruffling the feathers, and turning around in the nest, the female flew off. The male came 6 minutes later. He went to the usual perch and to the nest twig, and he seemed unaware that the female was gone until he perched on the nest rim. Then he peered into the nest, straightened up, and uttered a call, *chuck-hu, chee*. This call, the last part of which is the mate call, was repeated over and over. The male looked into the nest, even tried to feed, and then straightened up to call. After several of these efforts he crossed the nest to the opposite north rim. He looked under the nest, then got under it and searched, and finally returned to the south rim where he again called. Finally, he flew off and called out of sight about 50 feet from the nest. He returned to the nest-tree, again followed the path to the nest, and attempted to feed. Then he left and searched through all parts of the tree within 4 feet of the nest. He flew away again and called from 50 feet away.

Again the male returned to the nest-tree and went to the nest where he repeated the search and attempted feeding as well as repeating the calls. This time he flew off to a tree 40 feet away to call for the female. Two goldfinches flying about 100 feet away attracted him, and he flew after them, uttering the location note. Presently, he called in a tree 40 feet from the nest in another location. Still the female had not returned. At 5:33 the male went to the nest-tree from the north and called as he arrived at the nest from a perch 3 feet away. He perched at the edge of the nest and called; he then tried to feed in the bottom of the nest, but there was no female.

Two minutes later the female flew down to the nest from the west. She fluttered her wings a great deal as she arrived. The male began to feed her as she stood on the west rim and he on the south rim. The feeding took about twice as long as usual. Both birds appeared to be excited at seeing each other. The female went off after the feeding. The male went to a

perch 2 feet away where he called, but the notes were short and reassuring. The female did not answer. The male did not hop about as usual when inviting the female to accompany him, and after a minute he flew off out of sight. The female remained quietly on the nest.

The male had been greatly disturbed at the absence of the female. He actively hunted for her and appeared to be lost without her to receive the food he had brought and to provide the segments of the behavior that would release him to go on another foraging trip. Without the proper chain of events he was completely unable to proceed with his normal behavior. Especially striking was his failure to recognize that the bird he was to feed was not in the accustomed place. He even attempted to deliver the food anyway.

Approach to nest by male.—Watching at a nest in early stages of incubation was begun at 5:20 A.M. on May 26, 1939. Trips by the male to feed the incubating female were uniformly similar, with small variations, and with clear responses to disturbances and happenings at the nest. Also, through the whole period there were appreciable changes in his program from day to day. The first trip to the nest came 22 minutes after the start of watching. The singing male approached the nest and he stopped on a level with the nest 8 feet away on the uphill side. He sang there and flew to the nest-tree where he sang again. He moved down a limb a foot below and 6 inches away from the nest and sang. He then went to the south side of the nest where he perched and fed the female.

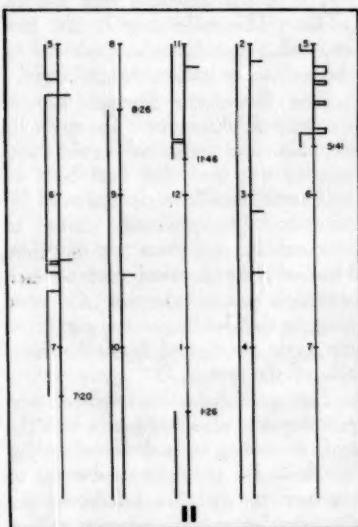
On the second feeding trip at 6:26, the male came to the nest-tree from the north without singing, and he went to the nest by the route used earlier.

In midafternoon the male came silently to the nest-tree from the east and perched 3 feet above the nest. He hopped down to a twig 3 inches from the nest and then to the side of the normal one followed earlier. The

Fig. 11.—Periods on nest by female Lawrence goldfinch in incubation, June 9, 1939. Observation from 5:00 to 7:20, 8:26 to 11:46 A.M. and 1:26 to 5:41 P.M. On right of the columns are indicated eleven trips to the nest by the male.

the nest. This approach deviated from female looked up as the male arrived, but she did not shake her wings until he was at the rim.

In bringing food to the incubating female the male never approached the nest from below; he always came from above. At first he followed the same path through the tree to the nest. He did not always land first in the same part of the tree, and this sometimes necessitated his moving through



the tree to get onto the regular path. Thus the trail first established through the tree was not always followed for the whole distance, but the last part of it, near the nest, was followed regularly. The route followed by the female to the nest was different from that used by the male. At a midday approach on the third day of watching the male arrived quietly and perched for a minute 8 feet above the nest. He descended to the nest, but he did not get onto the regular route until he was within 8 inches of the nest. On later trips that day the path was followed for its full length.

After the middle of the morning on the third day of watching, the male came to the nest-tree and perched motionless in the top for nearly a minute. He flew to a perch 3 feet below the nest, looked about, and then flew up to the beginning of his regular path which he followed to the nest.

The male went to the nest at 2:54 P.M. He landed on the perch 4 feet above the nest and chirped there twice. The female answered with a note, *wheet*. The male went to the nest and called three times on the way. At the nest more calls were exchanged.

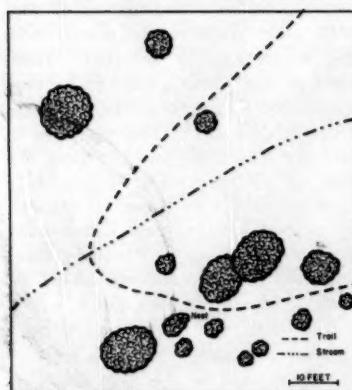


Fig. 12.—Diagram of surroundings of nest of Lawrence goldfinch studied on June 23, 1939.

same approach twig to the nest. There were other possible avenues to get to the nest, but he never used them.

At a nest observed in early morning on June 23 the first trip with food was by the male at 5:11. When he flew past the nest, the female began to call to him and he replied. The sounds were mostly location notes and mate-calls. The male then flew to the nest and landed 30 inches away in a peripheral twig cluster. Next, he began to work toward the nest along the nest limb. The last stage was on a horizontal approach-twig above the nest. The male hopped and sidled along this to feed the female. She raised her head and quivered her wings as he reached the approach-twig. After the feeding the male flew about 3 feet away and the female got off the nest to perch near him. Both then flew to a tree 15 feet away and moved out of sight. The female reappeared a minute later flying toward the nest and followed by the male 10 feet behind. She lit on the nest limb 8 inches from

June 9 was the fifteenth day of watching at this nest. The male by that time had ceased to use the pathway to the nest that had been so well established in early stages of incubation. He gradually came to approach the nest from any direction. However, the terminal part of each approach was always over the same twig, so that feeding was always from the same perch and from the same side of the nest.

The same habit of approach was prominent at a second nest where the male in coming to feed the incubating female had a generally used route to the nest, but he always followed the nest, but he always followed the same side of the nest.

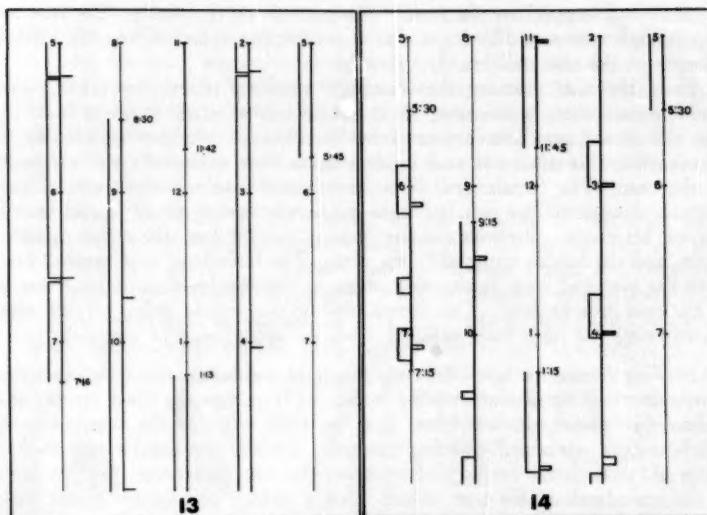
the nest and hopped to the nest. She paused on the rim of the nest to inspect the contents and then got into it and became quiet. The male landed 4 feet from the nest and then flew away.

Early the next morning the observer's watching station, in a tree, may have been too close to the nest, for the male was reluctant to go to it. His first call notes were not answered by the female. At his second try 5 minutes later his mate call and location notes were answered by the female on the nest. The female flew off a minute later and met the male. They went to an adjacent live oak and there the female flew at the male and forced him off his perch. She followed the male to another tree where they hopped about, and the female returned to the nest. The male went to a perch 2 feet from the nest and then to the nest where he fed the female. After a pause in the nest tree he left. This irregularity of the female going off the nest before being fed must have resulted from the disturbance of the man.

Feeding female on nest.—In early stages of incubation the male feeds the female on the nest at each trip he makes. He pumps the food up pigeon-fashion by heaving the shoulders, then his beak is inside the female's beak which is wide open and pointing upward. Usually the female quivers her wings all through the feeding. Sometimes the wing quivering starts as soon as the male lands in the tree. Once when a strange pair landed in the tree, the female began wing quivering, but she stopped when the birds came near. In a feeding in early afternoon there were 14 shoulder heavings. Before the feeding the female opened and closed her beak rapidly, but the observer could hear no sound. At a feeding in midafternoon the male stood up tall as the female reached upward when he came to the nest.

On the third day of watching, calls were exchanged between the members of the pair at a feeding at the nest in the afternoon. At the next feeding the observer heard chips from the pair 10 feet away as the female quivered her wings. Once, the feeding of the female involved some shaking of the head from side to side by the male, as if to aid in casting food into the bill from the gullet. In another nest watched at close range the female turned her head sideways and opened her bill. The male perched on the rim kept his head straight in line with the body, but poked his bill into the female's mouth and withdrew it. After the feeding the male uttered a short *whit*, flew to a near-by perch, called *whit* again, and flew away. This note seemed to indicate the completion of the feeding.

One male in midday approached the nest-tree and went down to the nest by way of a regularly used path. The female made chipping sounds as the male fed her. She pecked at the male's beak, opening and shutting her bill rapidly. The male regurgitated the food, which he held in his bill until the female took it. The female did not hold her bill open as do the young. After the feeding, the male went off the nest and sang. The female flew off 2 feet from the nest. The next day at 5:12 A.M. the male was at the nest. He fed the female and then turned and hopped to a horizontal perch close to the nest. As he left, the female went off the nest, with a flutter of wings, to the rim and then to the perch. As the female went onto the perch, the male flew and the female followed. Early in the morning the male was at the nest. He had not been there more than 15 seconds, but he was just



Figs. 13, 14.—13. Periods on nest by female Lawrence goldfinch brooding and feeding nestlings, June 23, 1939. Observation from 5:00 to 7:16, 8:30 to 11:42 A.M. and 1:13 to 5:45 P.M. On right of the columns are indicated six trips to the nest by the male. 14. Periods of feeding and brooding nestlings by female Lawrence goldfinch, July 4, 1939. Observations from 5:30 to 7:15, 9:15 to 11:45 A.M. and 1:15 to 5:30 P.M. On the right of the columns are indicated eight trips to the nest by the male.

finishing the feeding. The female was working her bill, as the male was backing away and working his. The male flew off to the twig-perch 6 inches south of the nest; then the female flew off following him. Five days later on June 7, the male flew into the tree 8 feet from the nest. The female uttered the ringing call in recognition of her mate and the male flew to a perch 3 feet from, and 1 foot above, the nest.

Miss Emily Smith (MS) recorded the history of a nesting pair of Lawrence goldfinches in San Jose in 1945. Nest-building was seen in a yew on April 3. The female was on the nest on April 9. The next day there were four eggs and the male was feeding the female on the nest. On April 24 there were three newly hatched young and one egg. On May 3 the female fed audible young. On May 10 three young were out of the nest at 5:00 P.M.

At another site where there were two recently hatched young, the male arrived at the nest tree at 7:00 A.M. on July 4 and perched on a twig 12 inches east of the nest. He called and waited 10 seconds before moving to the nest. The female began beating her wings rapidly and moving her tail up and down as the male arrived at the perch. She tilted her head back when he fed her. The male paused before the several feedings and opened and closed his bill several times until the food appeared. When the male left, he perched 30 seconds at an old black oak tree 20 yards north of the nest and then continued north with the tinkling call.

The next feeding trip came $2\frac{1}{2}$ hours later when the male perched on a twig of a blue oak 15 feet north of the nest-tree, looked about, and called four times. The female had begun to quiver her wings, but this changed to a beating when the male flew to the nest tree. He perched 24 inches from, and 6 inches above, the nest 20 seconds before flying to the nest. He regurgitated five times when feeding the female. Then he perched 30 inches from the nest for 15 seconds and flew away. The female started to feed the young 3 minutes after the male arrived. Between feedings, the female moved her head to a horizontal position, but the observer could not see the attendant activity because the bird faced away from him. She brooded for 30 more seconds and then flew off with the tinkling flight song.

An hour and a half later the male came to the nest tree and perched 40 inches above, and 30 inches from, the nest for 10 seconds. He moved to the nest and fed both young and the female. He perched on the west side of the nest, moving to three different perches in 8 seconds and then flew.

Male accompanied by other birds.—On the first three days at a nest where incubation was taking place, the male, on visits to the nest, was often accompanied by other goldfinches. These were generally males, but sometimes pairs flew with him, and occasionally only a female. On the eighth day the male was never accompanied by other birds. At a trip to a nest where incubation was in progress early in the morning, the male was accompanied by another male. They lit in a peripheral twig cluster 30 inches from the nest. Then the owner flew at and drove away the other male which paused momentarily in another tree 15 feet away.

Departure of male from nest.—On May 25, at 6:00 A.M. the male arrived in the tree 10 yards from the nest, and then after first calling he was answered by the female, went to the nest, and fed the incubating female. After wiping his beak, the male sang a little in the nest-tree; in less than a minute he moved to a tree 20 yards from the nest and sang for 2 minutes more. Then, singing in flight, he settled on a tree about 35 yards north of the nest, stopped and sang for a moment, and then made off, still singing in flight out of sight to the southeast.

After feeding the female late in the morning on May 28, the male left the nest, paused on the usual perch 2 feet east of the nest, then flew to a perch in a tree 20 feet north where he sang twice. A wiry location note seemed to be coming from the female on the nest. After seven of these calls the male flew off through the trees out of sight, but the female did not leave the nest.

In midafternoon after feeding the female the male perched 2 feet east of the nest. The female went off the nest and perched above the male and 2 feet away. She then dived at the male which flew 6 inches lower. The female dived again and the male flew 3 feet away. The female then went to a tree 10 feet northeast of the nest. She moved about 5 feet to a place where she wiped her bill on a branch, ruffled her feathers, hopped along the limb, and flew back to a perch 6 feet above the nest. The male below her flew up in an arc to her level and then dropped back down. The female then went to the nest, and the male went to his original perch 2 feet from the nest. He next sang twice and flew off out of sight. After the next feeding the male

did not sing until he had gone about 25 feet from the nest. Then he sang twice and flew away.

Behavior of pair after normal period.—After the end of the normal incubation period at the nest where the two eggs failed to hatch, the program of activities became irregular. As the nesting behavior began to break down, the birds failed to follow the earlier program, but evidently the eggs remaining in the nest held them to the main part of the routine of incubation behavior. For several days the female spent much time standing in the nest and bending her head beneath her body. What she did could not be clearly seen. She may have been looking at, or working at, the nest lining, the eggs, her feet, or her brood patch.

In one example, at midday, the female stood up and looked at the eggs for about a minute. She then preened her wing and looked at the eggs again. She appeared restless, the male had not brought food for 1½ hours. Five minutes later she pecked hard at the nest bottom or something in it. In early afternoon the female was restless and she inspected the nest contents frequently for periods of almost a minute. She also frequently worked at the interior of the nest with her bill.

Other happenings on the afternoon of the seventeenth day of incubation showed weakening of the rigid incubation program. At 2:16 the male was in a live oak, 20 feet from the nest, uttering location notes and being answered by the mate call from the female. She did not stop inspection of the eggs or nest interior. When two goldfinches flew near by, the male flew out after them and all three perched in a tree 50 feet from the nest. The male presently returned to the first tree and then he flew to a perch 3 feet from the nest. As he went to the regular approach twig, the female was looking in the nest, and she did not look up or quiver her wings, even when the male was only 1 foot from her. As the male moved to the nest, the female looked up, sank in the nest, and quivered her wings to be fed. After feeding, the male moved away 2 feet from the nest and called twice, but the female did not answer. After he flew 100 yards away, the female uttered the mate call a few times, but she did not follow him. The urge to follow the goldfinches had interrupted the feeding trip. For the first time, the female failed to quiver her wings as the male landed on the approach twig.

After the male left, the female resumed the preening and egg inspection. At 2:52 the male arrived and perched for 45 seconds at the beginning of his new route to the nest. He did not call and the female seemed not to notice him, except that several times she jerked her wings at the sides. She did not quiver them. The male flew off, and uttered ten or more location notes.

In 6 minutes he was back and on the usual perch, and then he moved to the approach twig where he fed the female. She quivered her wings as soon as the male arrived in the tree, although he was on the perch used previously. The female faced away from the male both times. Apparently the male hesitated to approach the nest when there was no wing quivering. After the feeding, the male moved to a perch 2 feet away and gave both location and mate calls. The female answered with the mate call, but she did not leave, and the male flew off out of sight. The female wiped her bill on

the nest rim. She then began to watch the nest contents as she faced the southeast and shaded the nest.

Two minutes later, calls by a pair of goldfinches in the top of a tree 40 feet from the nest brought no response from the female. She spent four-fifths of her time looking down at the eggs as she shaded them. In 15 minutes the male came to the perch 2 feet above the nest. He hopped and flew a foot below the nest, then found the approach twig, and followed it to the nest. When the male arrived in the tree he called, *whit*, and the female answered with a mate call. She began to quiver her wings before the male got to the approach twig. After feeding, the male waited 2 feet away and the female came off. She flew near him to the north side of the tree and then to a tree 15 feet southwest of the nest. There she hopped about and wiped her bill before returning to the approach twig and into the nest. The male had remained below the nest. He then moved nearer the nest and called the female with a location note, and *whit*. The female answered three times, but she did not come away again. The male then called unsuccessfully from 20 feet away. He went 10 feet farther and called, but the female was looking into the nest and did not respond. Obviously he had tried to coax the female on a long flight, but she would not leave.

At 5:05 the female pecked in the bottom of the nest and she brought up a down feather. She placed it on the rim, then picked it up and worked it into the lining 2 inches from the first location. Movement of the head was from left to right with the quill to the right. The female was not incubating, but she stood facing the sun. Ten minutes later the female was restlessly watching the nest-interior and working there with the bill while she stood facing south in the nest. The male had been gone an hour.

Two days later, on the nineteenth day after watching began, the female was still incubating. On the twenty-first day the nest was deserted and the lining was becoming loose, but the two eggs were still present. Evidently the pair had been unable to prolong the incubation behavior longer than the seven to nine days past the twelve days which is probably the normal length of incubation for this species.

YOUNG

Feeding of the young in the nest is at fairly uniform hourly intervals. This might be regulated by the time required to gather and prepare the food, and also it might be influenced by the hunger limits on the part of the bird to be fed. Through the 11 days, before the two young left the nest on July 14, in 109 hours we recorded 139 feedings by a parent bird. On nineteen occasions the male fed the female. Feedings on the first 4 days numbered 6, 7, 4, and 1, and there was one on the last day. This represents the time required to change from the program of incubation in which all the food brought to the nest was delivered to the female and she ate it. For a few days after hatching the tendency was for the female to take the food and then deliver it to the young after the departure of the male. The male had great difficulty in reaching past the begging female to get food to the young. When it was no longer necessary for the female to brood the young, she accompanied the male on trips for food. The parents then tended to arrive at the nest together and to take turns feeding the young. In the early days

TABLE 4.—Record of Lawrence goldfinch nestlings

July	Hours Watched	Trips by Parents	Feedings
4	9	15	19
5	10	15	18
6	9½	14	18
7	11	18	18
8	10	16	17
9	8½	13	13
10	9½	18	16
11	10½	21	21
12	10	20	22
13	10	20	18
14	11	18	14
Total 11 days	109	188	194

the male nearly always fed first, but later the female delivered food first almost as often as the male did. The male fed the young 69 times; the female, 51 times. On 60 feedings only one parent fed the young. Sixty feedings took place when both parents came to the nest at the same time. The male fed alone 25 times, or 1 to 5 times daily. The female fed alone 35 times on seven days. She fed 11 times on the first day and on the next 4 days 7, 7, 5, and 3 times. On the trips together the male fed the young first 44 times, but none on the first day; the female fed first 16 times, only twice in the first 6 days, and 14 times in the last 5 days.

In 1939 a nest was found in early afternoon of July 2. The nest contained two young birds and it was studied daily until July 15 when the second of the two young contained in it left. From 9 to 11 hours daily were spent watching the development of the young and their care. Although it was not determined for this nest, we assumed that the young birds hatched on July 2 and that they left on the 13th or 14th day after hatching. According to Walkinshaw (1938-39:16) the female American goldfinch broods the young through their 4th day in the nest. Possibly our Lawrence goldfinches hatched on July 3.

Abbreviated extracts from notes on the developments at the nest show the changing character of the nesting for some of the days when observations were made.

July 2, 1939, 2:00 P.M.—The female was sitting on a nest, and she could not be dislodged by an observer. She was spread out so that she completely covered the cup of the nest, with only her head and tail showing above the rim. She raised herself somewhat so that she could look down into the nest and to rearrange breast feathers. The observer could see a fluff of downy white feathers but could not tell whether they belonged to her or to a nestling.

July 4, 1939, 5:30 A.M.—The female was visible on the nest. At 5:52 she moved about on the nest, raising the body when doing so, and thus becoming visible above the rim. The entire tail projected over the north rim. At 5:55 she moved about on the nest again, looking into the nest in front of her as she did so, but she did not change position. At 6:00 she raised her body from the nest and moved backwards slightly, tilting the crissum and tail upward 20°. She worked in the bottom of the nest directly in front of her for 10 seconds, and then raised the body slightly, before she moved forward and settled. At 6:11 the female left the nest and flew west. The male had fed her at 6:08 and she appeared to be feeding young in the nest. She moved back so that she was almost perched on the rim, and then she worked her bill before putting her head down into the nest.

She did this seven or eight times and then left the nest. At 6:38 the female returned to the nest from the west. She gave a loud call when she alighted at the tree and waited 10 seconds before flying to the nest. She approached the nest cautiously, watching the observer in the top of a neighboring blue oak. The two young in the nest raised their heads and opened their bills, but she did not feed them before settling on the nest. At 6:43 the female flew from the nest immediately after feeding young. The eyes of the young were closed, being large purplish blue and extending from the dark pink skin of the head. The interior of the bills was red. Down feathers were well developed along the spinal tract, the only part visible, but none was seen in the head region. The female had been brooding for 5 minutes. When the female was at the nest, the young huddled in the bottom, moving only slightly without raising their heads. At 6:58 the female returned. She alighted at a twig 10 inches from the nest, waited 5 seconds, and then flew to the nest where she paused momentarily before stepping carefully into it and settling down over the young with little up and down movements to find the right position. She did not feed young them even though she looked down into the nest before entering. She was not motionless on the nest, but she squirmed about somewhat and occasionally flicked the wings and tail. At 7:10 the female flew west after feeding young for 1 minute. As before, she backed in nest and fed the young in front of her. She settled back onto nest after feeding. At 9:18 she faced west on the nest and fed the young. She settled forward on the nest when through and spread her wings, effectively shielding the nest from the sun's rays. She sat low on the nest, so that her back was $\frac{1}{4}$ inch above the rim. She raised her body $\frac{1}{4}$ inch from the nest, poked into the nest with her bill, and looked about.

July 9, 1939, 6:25 A.M.—The male and female arrived at the nest-tree from the northeast. The male perched 10 inches east of the nest for 10 seconds while the young reached high in the nest. The male moved to the rim and fed the young, leaving them abruptly when through and perching 4 feet above and 5 feet southwest of the nest, while the female, who had been perched 2 feet south and 18 inches above the nest since alighting, flew to the north rim of the nest and fed young perfunctorily, compared with feeding by the male. She paused with head just above heads of young when through feeding. This holding the body motionless after feeding followed by looking around at the nest was quite distinctive of the female. The male left hurriedly when he completed the feeding. The female perched at the side of the male for 10 seconds, and then they flew west. Over the center of the ravine they seemed to fly straight up 1 foot, touch bills together, and hover for a second before continuing flight to west. At 6:45 A.M. the young were visible over the rim of nest only when the adults were present.

July 10, 1939, 5:36 A.M.—The male and female arrived at the nest tree from the west. The female perched 2 inches north of nest for 30 seconds and then perched on the rim and quivered her wings. The *sweet* call had been started before she reached the tree. The movement of quivering the wings was least near the shoulders and greatest at the tips. The male perched briefly at three locations in the tree and then flew to the rim of nest. He fed only the young, but the female begged also. She turned her head toward the male, tilted her head back 10° , and opened her bill. She quivered her wings so that the wing-tips moved $\frac{1}{4}$ inch. The male perched 2 feet northwest and 18 inches above the nest while the female remained perched on the rim, wings still quivering, but not violently. The young begged in front of her and she fed them 15 seconds after the male left. She remained motionless 10 seconds after feeding the young and then looked about. The male sang intermittently the whole time. The female left the nest and flew northeast, followed one second later by the tinkling male. At 8:43 the male and female returned to the nest from the northeast. The female perched 6 inches east and 3 inches above the nest for 45 seconds and then moved to the south rim of the nest where she perched, quivering her wings and calling *sweet*. The young begged from her and also called. The male moved to the north rim of the nest 2 seconds after the female arrived and he fed the young, the female begged but got no food. The male flew up 30 inches and 18 inches southwest where he perched and began to sing. The female remained at the perch and quivered her wings with the bill held slightly opened. After 30 seconds, during which the young reached up and grasped her bill several times, the female fed the young intermittently for 15 seconds. She seemed listless and moved to the east rim and quivered her wings violently and spasmodically, after having perched motionless for 5 seconds after feeding. The quivering of wings began when the male began tinkling. He stopped tinkling at 8:46; the female stopped wing quivering, pecked at rim of nest,

and looked at the young. She flew northeast at 8:46 followed by the male. Both were tinkling.

At 9:35 A.M. the young in the nest preened themselves. They had been on the north rim since 8:55 but returned to the nest at 9:30. At 9:41 one of the young climbed up on the rim. At 9:55 the young climbed into the nest. At 3:45 P.M. the young were rapidly becoming adult in appearance; the bills were losing the wide appearance and were lengthening; they appeared entirely feathered; the only down remaining was the circular patch on top of the head.

July 11, 1939, 5:30 A.M.—The male came to the nest tree from the west. He perched 18 inches west southwest of, and 3 feet above the nest, for 30 seconds and then flew to the rim of the nest and fed young; one received twice as many feedings as the other. It was closest to the male and also it reached the highest. When through feeding, the male perched 30 inches northeast and 8 inches above, the nest for 15 seconds while he looked about and gave the male call twice. He began the tinkle song 1 second before leaving. He flew northeast with the tinkling flight song. At 6:07 the observer heard the tinkle song to the south, and the young began the *sweet* call. At 8:53 A.M. the young bird on the rim of the nest preened the feathers of its right wing. Just as the female flew down to the nest rim, the young beat their wings vigorously. There was a narrow brownish yellow band on the wing above the wide band, the two being separated by a dark gray band. The young on the rim preened the back near the rump and then preened the right wing thoroughly. At 9:14 both the young were on the north rim of the nest. The breasts of the young were a light yellowish gray. At 9:25 one of the young got back in the nest, the other on the northeast rim. The bills looked larger than those of the adults. 9:27 the other young climbed back up on the north rim. 9:29 the observer heard a tinkle and saw the adults fly to the valley oak from the southwest through the foliage of other trees. At 9:31 one of the young flapped its wings three times, calling. The down was nearly gone from the head, only a tuft remaining at each side. At 9:34 the male perched 2 feet south, and 20 inches above, the nest. The young begged insistently, and the female finally stopped quivering her wings and fed the young, but immediately she began quivering her wings again. When the male flew towards the nest, the female dropped down to the north rim where she crouched facing west with head thrown back to a 25° angle, and with wings quivering. The male landed where the female had fed the young; he fed each of the young once, and then dropped to the east rim and continued feeding. When finished, the male flew to a branch 3 feet northeast and 10 inches above the nest, sang for 3 or 4 seconds, and then tinkled off to the northeast followed by the female. The young birds climbed up on the north rim again 10 seconds after the adults left. At 9:53 one of the young climbed 2 inches above the nest on an upright limb at the north rim of the nest. The other young went back into the nest. The one on the limb preened its feathers. The tail feathers were not more than $\frac{3}{8}$ inch long. At 9:57 the young climbed down to the rim of the nest. The contour feathers were quite fluffy. At 10:03 the young on the rim of nest had preened almost incessantly. At 10:04 the young one on the rim beat its wings rapidly for 3 seconds. At 10:05 both young were on the rim. At 10:27 the young in the nest began *chee-up* call.

At 10:28 the adults flew to the nest tree from a valley oak across the ravine. The female perched 3 inches north of nest and the male perched 10 inches below and 12 inches north of the nest. The female moved to the rim of the nest and the young, who had crawled down into the nest upon arrival of the adults, begged to be fed. The female was unmoved by their pleading for 10 seconds, and then she fed them, remaining perched at the north rim after feeding and quivering her wings. The male sidled along the branch 6 inches and then flew to the southeast rim of nest and fed young, the female begging for food but not getting any. The male flew 30 inches northeast and up 12 inches and perched. He began to sing and then tinkled, whereupon the female flew northeast closely followed by the male. At 11:04 both young in the nest were busy preening. At 11:06 one of the young took 5 seconds to climb up on the north rim of nest. At 11:09 the young stopped preening and began calling. At 12:45 the young were on the rim of the nest. At 1:18 the young in the nest preened feathers. At 1:32 the adults tinkled across the ravine. The young began calling one minute later. At 1:50 one of the young climbed up on the rim, the other was facing south inside the nest. At 1:52 the one on the rim moved to the northeast rim and the one in the nest climbed onto the north rim. The one on the north rim flapped its wings rapidly for 2 seconds. At 2:05 both of the young were on the north rim, busy preening, keeping up an incessant

TABLE 5.—Nature of 139 feedings by Lawrence goldfinches through 11 days before 2 young left nest

Date	Young fed by					
	♂ Only	♀ Only	♂ First	♀ First	♂ fed ♀	
4	2	11	0	0	6	
5	1	7	3	0	7	
6	2	7	2	1	4	
7	5	5	3	0	1	
8	2	3	5	1	0	
9	1	0	6	0	0	
10	2	0	6	1	0	
11	1	0	6	4	0	
12	2	2	5	5	0	
13	3	2	5	2	0	
14	4	0	3	2	1	
Total 11 days	25	37	44	16	19	

tsee, tsee. At 2:26 one young bird climbed back into the nest. At 2:40 the young began *chee-up* call when the adults perched in a blue oak in the vicinity of a wood pewee's nest.

NEST-CLEANING

At the nest watched daily for eleven days beginning on July 4, 1939, the young birds were approximately two days old on July 4. The rim of the nest then had a considerable amount of fecal matter on it. This indicated that the incubating female had not regularly left the nest to defecate. She was first seen removing a fecal sac from one of the young at 10:26 A.M. At 5:00 P.M. the female reached back into the nest and appeared to eat a fecal sac. This was repeated four times and then again at 5:06, after she had fed the young.

The next morning at 6:23 the brooding female moved to the rim of the nest and fed the young. She then sidled around the nest to the opposite side, looked about and into it, picked up a fecal sac and flew with it. This time the flight song seemed less loud than on the other occasions. At 9:05 the brooding female reached back to the left under her raised wing and picked up a fecal sac. She moved her head to a forward position, put the wing down again, and ate the sac. It was a small one, and she swallowed it in one gulp. An hour later after both parents had fed the young, the female settled on the nest, but immediately she got onto the north rim by backing onto it and sidled around to the southwest side. She looked into the nest, and soon the posterior of one of the young appeared and the nestling defecated. The parent took the sac as it emerged. She immediately swallowed it and then settled on the nest, but she left in 10 seconds. At 11:23 the female stood in the nest, looked down into it, turned, faced the west, reached down, and picked up a fecal sac. She flew off down a ravine toward the north with it, but with no flight song.

In the afternoon, at 2:09, the female ate three fecal sacs that had been on the north rim of the nest. Half an hour later she fed the young and settled

TABLE 6.—Care of young Lawrence goldfinches in nest

July	Trips	Male			Seconds feeding			Minutes interval		
		Seconds at tree			av.	min.	max.	av.	min.	max.
		av.	min.	max.	av.	min.	max.	av.	min.	max.
4	8	75	30	180	24	12	45	52.2	32.5	63.5
5	8	90	30	180	25	10	45	109.2	53.5	258.5
6	7	105.7	50	240	15	5	25	72.8	55.0	97.5
7	9	135.0	45	690	13.4	5	20	68.3	2.25	120.0
8	9	101.7	30	240	10.8	5	20	57.0	2.0	108.5
9	7	94.3	90	120	10.7	5	15	61.0	56.0	67.5
10	9	136.1	30	390	7.4	5	15	65.5	33.5	128.25
11	11	91.4	30	180	7.1	5	15	61.2	40.5	88.0
12	12	67.5	15	150	6.3	4	10	48.6	27.3	63.5
13	10	156.0	45	570	6.1	3	11	55.2	25.5	82.25
14	10	126.5	5	570	5.0	2	8	66.6	39.5	147.0

July	Trips	Female			Seconds feeding			Minutes interval		
		Minutes brooding			av.	min.	max.	av.	min.	max.
		av.	min.	max.	av.	min.	max.	av.	min.	max.
4	7	12.5	2.5	19.5	43.3	10	60	37.2	15.0	55.0
5	7	23.9	3.0	57.5	42.5	15	70	44.9	4.5	77.5
6	7	6.7	1.0	17.5	18.5	10	35	51.8	22.5	68.5
7	9	32.4	1.25	69.0	13.8	10	20	49.0	2.0	83.0
8	7	52.2	48.5	55.0	10.1	4	20	34.6	1.0	58.0
9	6	---	---	---	7.0	5	12	60.8	56.0	67.5
10	9	---	---	---	8.4	5	15	65.5	33.5	128.25
11	10	---	---	---	6.4	3	10	55.9	40.5	88.0
12	10	---	---	---	7.6	5	11	49.5	34.8	63.25
13	10	---	---	---	6.7	4	11	55.2	25.5	82.25
14	8	---	---	---	7.2	5	12	80.1	39.5	147.0

on the nest. She then picked a fecal sac off the rim and ate it. After that she picked at something in the bottom of the nest, stood up and looked around. She climbed up on the rim and flew off with a flight song.

FEEDINGS OF YOUNG

THREE-DAY OLD (JULY 4, 1939)

1. Female fed young after male fed her at 6:08 A.M. She moved back so that she almost perched on rim and then worked bill before putting head down into the nest. She did this 7 or 8 times and then left.
2. Female fed young 5 minutes after she returned cautiously and went onto nest without delivering food, even though the 2 young raised their heads and opened their bills. She flew away immediately after the feeding.
3. Female fed young 5 minutes after male fed her, settled back on nest, and left a minute later.
4. Female fed young and settled on nest.

5. Female fed young $3\frac{1}{2}$ minutes after male fed her, then brooded the young 30 seconds before she flew away.
6. Male fed both female and young; perched on west side of nest and moved to three different perches in 8 seconds before he flew away.
7. Female fed young 3 minutes after male left. Head moved up and down about every 2 seconds. She moved back slightly when feeding and forward again after feeding.
8. Female fed young for 30 seconds after 6-minute interval.
9. Female fed young as soon as male left after feeding her, and then she flew away.
10. Female arrived quietly 57 minutes later, fed young and settled on nest. Then she stood and fed them for another 5 seconds before settling again.
11. Male perched on side of nest, ignored the female's begging, and fed the young. He left and the female followed half a minute later.
12. Female arrived and fed young 45 minutes after the male fed them.
13. Male arrived in 10 minutes and fed female only.
14. Female fed young a minute after departure of male. She stood in the nest and fed the young directly in front of her as they held their bills in the air. She then left.
15. Male fed young when female was absent on his arrival, and he left immediately.
16. Female fed young for 40 seconds, 8 minutes after her arrival.

In midday on July 4, 1939, the male fed the female on a nest and then perched on a small branch 2 feet from the nest. He stayed for about 15 seconds and then flew, but the strong wind blew him off his course. The female quivered her wings until the male flew away. The strong wind moved the branch that held the nest.

At a nest where young were being fed, arrival at the nest and departure were decidedly different. Arrival was quiet and inconspicuous. The departure was by an undulating, open flight, accompanied by the tinkling flight song. These differing mannerisms would be useful for safety. The quiet approach does not draw attention to the nest or to the adult. The departure, however, draws attention away from the nest and makes the departing bird conspicuous. The male did not approach quietly, but he was quiet at the nest.

In the afternoon the male came to the nest when the female was absent. He perched 2 inches below and 6 inches north of the nest. He called *aaaah* five times and looked about. Once he appeared ready to fly away, but he turned and hopped to the rim of the nest and fed the young from there. He stopped once and looked about for 3 seconds, and resumed feeding. After he fed he called once and flew toward the east.

FOUR-DAY OLD (JULY 5, 1939)

1. Male arrived at 5:25 A.M., fed female on nest, and left. Female remained on nest.
2. Female alternately fed young from rim of nest 5 minutes after first arrival of male. She then settled on the nest.
3. Female fed young after male fed her; she then picked up fecal sac from rim of nest and flew away with it.
4. Male fed female and both young as he perched on rim of nest and left.
5. Female stopped wing quivering half a minute after departure of male, stood up in nest, fed the young alternately, and settled back on the nest. She immediately got up, took an extruded fecal sac, ate it and again settled on the nest.
6. Male fed female after both arrived at nest together.
7. Female stood in nest and fed young a minute after departure of male. She then settled on the nest.

8. Female fed young, settled on nest for 5 seconds, and then stood in the nest and fed the young for an additional 10 seconds.
9. Male came to nest while female was absent; he fed the young, and flew away.
10. Female stood up 2 minutes after her return to the nest, fed the young, and settled on the nest again.
11. Male fed female only and left.
12. Female stood up in nest 2 minutes after departure of the male and fed each young bird at least 15 times, and then left.
13. Female fed young on arrival after absence of more than an hour and settled on nest.
14. Male fed female and young on return after absence of 104 minutes; female tried to get all the food. Male left 3 seconds after feeding.
15. Female fed young, pecked at inside of nest for a minute, and flew off with flight song.
16. Pair arrived at nest together; male fed young and female without interference from latter.
17. Female fed young 5 minutes after departure of male and after 8 minutes of brooding. She pecked inside the nest and flew away.

On the first trip the male flew to the nest, from the top of a hill, in large undulations. The bird turned abruptly when he reached the vicinity of the nest and entered a live oak 25 feet from the nest. He remained in this tree for a minute and then moved to a blue oak 20 feet from the nest-tree. For another minute he perched in the blue oak on a limb 6 feet lower than the nest site. While the male was in the live oak, the brooding female began calling the *sweet* note. From the blue oak the male uttered the usual announcing call. The female began to quiver her wings when the male called and also tilted back her head and raised the open bill. The male moved to the rim of the nest from a perch 10 inches away. He fed the female and at once flew away.

After the male had fed the female, he left and the female remained on the nest. A little more than a minute later (5:30) the female moved to the rim of the nest and fed the young. The feeding was calm and deliberate. The bird worked her bill once or twice between feedings as she alternated the feeding. When the feeding was over, she again settled on the nest. At 5:39 the female flew off to the northeast with a tinkling flight song. Twenty minutes later she returned from the south, paused at the rim of the nest, and looked in for 10 seconds before she moved onto the nest. She squirmed into position and faced toward the southeast.

In early afternoon the male came to the nest while the female was away. He perched on a branch 2 inches below the nest and 20 inches away to the north. After 2 minutes he sidled along the branch toward the nest. He perched on the rim of the nest and fed the young. The eager young birds at first reached up half an inch above the rim, but their eagerness diminished and the male had to reach down into the nest to feed the nestlings. At first he called loudly, but while feeding the young he made muffled sounds. After one tinkle call he flew away.

Twenty minutes after the male brought food to the nest and departed, the female arrived in the nest-tree. She perched in the near vicinity of the nest for half a minute before she moved down to the nest in a series of hops and then settled on the nest. Shortly she stood up and moved back slightly, and fed the young. The food was visible as she worked the bill between

feedings. The food had a pasty consistency and a creamy color. The female then settled back on the nest.

Shortly after 4:00 P.M. the brooding female raised herself to a half-standing position in the nest. She then lowered the head deep into the nest. She rose after a second and looked around before lowering her head again. This performance was repeated 21 times. The bird moved the tail up and down through a small arc (about 5 degrees) while the head was low in the nest. When the bird settled in the nest again, she bobbed slightly up and down four or five times. Possibly, this behavior indicated pecking at nest parasites.

FIVE-DAY OLD (JULY 6, 1939)

1. At 5:10 A.M. female stood in nest and fed young for 35 seconds and settled back in nest after pecking inside it 7 times.
2. Male fed female only, and both birds flew away.
3. Female fed young alternately two seconds after her return to nest.
4. Male fed female and flew away with flight song.
5. Female fed young two minutes after male fed her and she carried away a fecal sac.
6. Female came to nest, fed young, ate fecal sac, and departed.
7. Female arrived at nest, fed young, settled on them, and brooded.
8. Male fed both young and female; then he left.
9. Female fed young one minute after departure of male and flew off with flight song.
10. Female arrived, fed young, and settled on nest.
11. Male arrived and fed young only. Two minutes after the male's departure the female stood up and touched the mouths of the begging young with her bill, but did not feed them.
12. Pair arrived together and male fed female and then the young.
13. Female fed the young half a minute after departure of the male, making about 6 feedings in 20 seconds. She looked around between feedings, pecked in the nest afterward, and flew away.
14. Female returned after absence of more than an hour, stood in the nest, fed the young, and brooded.
15. Male arrived and fed young only, despite violent begging by female. He pushed her head aside or avoided her in reaching past to feed the young. Female followed him when he left.
16. Pair arrived at nest, the male 3 minutes ahead of female; male fed young only and ignored entirely the begging of the female. Male transferred the food quickly, not taking more than a second for each feeding, and alternating between the young. There were about eight feedings to each bird in 20 seconds.
17. Female fed young slowly after departure of male, with about 2 feedings each in 15 seconds. She then pecked at the nest rim three times and flew away.

SIX-DAY OLD (JULY 7, 1939)

1. Pair arrived at nest at 5:57 after a 40-minute wait; female begged, but male fed young 22 times and flew away.
2. Female fed young about 5 feedings each, 2 minutes after departure of male, and then she left.
3. Pair arrived together nearly an hour after the first arrival, and they remained for almost 12 minutes. Female begged and then fed the young 2 minutes after arrival.
4. Male fed young only, despite the begging by brooding female.
5. Female arrived, fed young, and left 4 minutes later.
6. Male fed young and left 10 seconds later.

7. Female arrived, fed young from rim of nest, and brooded for 57 minutes.
8. Male fed young after absence of more than 100 minutes.
9. Female fed young 104 minutes after her last feeding and after an absence of more than half an hour. The male had fed them about half an hour earlier.
10. Female arrived, fed young, and remained to brood them for 43 minutes.
11. Male fed both young and female, and female joined him as he flew away.
12. Pair arrived at nest together. Male fed the young three times each and the female fed them; then both parents left, the female in the lead.
13. Pair came again after an hour and 15 minutes. Again both fed the young, but the male fed first. They left together.
14. Male fed the young on a 2-minute visit to the nest.

EIGHT-DAY OLD (JULY 9, 1939)

1. Male fed young first, feeding a minute and a half after his arrival at the nest, but the female remained motionless on opposite side of the nest, and he did not feed her.
2. Both parents arrived at nest after absence of an hour. Male fed young and left abruptly.
3. Female fed young in perfunctory manner as soon as male moved, and then she paused with her head just above the heads of the young and body motionless for 10 seconds. Both parents then flew away.
4. Parents arrived together, the female perched on rim of nest calling and with wings quivering. In 5 seconds the male went to the nest and fed the young, even though the female opened her mouth and begged. He immediately flew to another branch and began to sing.
5. Female remained on rim of nest quivering her wings for 15 seconds and then fed the young. She flew off, closely followed by male.
6. After absence of an hour the parents came to the nest; the female landed first, but the male fed the young first.
7. Female fed young when male moved, and they flew off with female in lead.
- 8-9. Feedings much like last except female followed male in leaving tree.
10. Parents arrived together and perched for half a minute before male flew to nest and fed young.
11. Female moved toward nest and perched 3 inches away for 20 seconds while young begged and then she fed them. Her motionless pose was interrupted to pursue an invading blue-gray gnatcatcher.
12. Male went to nest first and fed young; then he perched 2 feet away and sang the whole time the female was at the nest.
13. Female went to nest as soon as male moved and she fed the young. She pecked at the rim of the nest and then flew off, immediately followed by the male.

Care of young.—On June 12, 1939, a young goldfinch begged from an adult female. The young one was neither fed nor driven away. Finally, the female flew away and the young one followed her.

On June 25, 1939, a male flew to a nest where he uttered two kinds of notes and a song. A young goldfinch in an adjacent tree flew to the male and forced him off his perch. The male dropped down through the tree and the young bird followed him and begged. The young bird followed the adult out of sight among trees, but got no food. The young bird was able to fly well. Its tail was ragged, but nearly of adult length. At 6:30 A.M. on July 3, 1938, an adult female fed a young bird out of the nest and perched on a wire. At 6:50 A.M. on July 22, 1950, a group of three goldfinches included one that begged briefly in dead willow branches.

A post-nesting flock of nearly fifty birds, both adults and young, was present through the early part of the afternoon on June 28, 1938, along the edge of an abandoned field. Close by, there was a parkland of oaks, a patch of chamise, and a wire fence, where the birds perched when not foraging on the ground. The flock kept in one small area. Mostly the birds were on the ground, apparently picking up the ripened seeds then available from many annual plants. There was much flying about and the food calls of the young were the most conspicuous sounds in the vicinity. The young birds appeared to outnumber the adults. They appeared to be feeding themselves part of the time, but nearly every adult was closely followed by one or two young birds. One young bird was begging from a male; a few minutes later one was begging from a female. Several young ones in chamise bushes pecked at the flowers, and two picked at leaves.

The feeding of young out of the nest by parents was taking place in a chamise bush on the morning of July 25, 1948. The parents fed continuously on the newly ripened seeds in the tops of the bushes. The two young birds spent most of the time at middle heights in the bushes, between the two adults, and changing perch from time to time. They uttered constantly a plaintive *chee* of descending inflection. One went to the female's perch to be fed just as a red-shafted flicker flew up, with much noise, from the ground in the vicinity. This disturbed the goldfinches and they flew into the air, circled, and lit in coast ceanothus. The juveniles followed the adults, uttered intensified cries, and quivered their wings when they lit near the adults. The goldfinches moved to a chamise bush. A young one lit 8 inches from the female and walked along the ascending twig, facing lengthwise of it and calling. As it approached the parent, its calls were intensified and it attempted to walk up her back, fluttering the wings and partly hovering. The female moved to a horizontal branch lower in the bush, and the young one followed and perched facing her on an ascending fork at such height that its body, held horizontally, was in line with the parent which it faced.

The young bird fluttered its wings in a wide arc, but the movement involved only the distal part. The calls were louder than those uttered previously. The female fed this bird by regurgitation, in about eight successive deliveries, between which she seemed to gulp more food. At these times the juvenile made the loudest of all calls and fluttered hardest. After this feeding the whole family flew off to another bush.

Early in the morning on July 12, 1941, a female fed a young Lawrence goldfinch in a road. The young bird followed her closely wherever she went. The white in its tail showed more conspicuously than in hers. She picked nutlets from fiddleneck and fed them to the young one. It would lunge at her, utter the tinkling call note several times, open its mouth, and rapidly flap its wings high over its back, all at the same time. The parent, standing in the road, at first backed away, and then it fed the young one several times in succession. Then both flew to the fiddleneck at the side of the road.

Early in the morning on August 1, 1946, an adult female accompanied a young bird as the two ate seeds from plants. They were silent except for weak *tsip-tsip* notes made by one as it foraged. Half a minute before the birds left the plants, the young one uttered a continuous series of medium-pitched notes with a somewhat nasal quality. The adult uttered one high-

pitched, two-parted note about one second before they left. Although this young one was clearly associated with an adult, it picked food from the plants. It was sometimes clumsy and lost its balance more than the adult did, but it was not fed by the parent.

One young goldfinch, only a few days out of the nest, carried food to a limb of a blue oak where it held the object under one foot and then pecked at it.

PLUMAGES

The juvenal plumage is similar to that of the adult female, with colors duller, with yellow especially on breast, less distinct, and underparts obsoletely streaked. Adult females are similar to adult males, but without black on head, the colors in general are duller, with yellow less distinct.

Adult male has anterior portion of head all round, including throat and fore-part of crown, black; above brownish gray (the back sometimes tinged with olive green), changing to yellowish olive-green on rump; sides of head and lateral underparts paler brownish gray, becoming white on under tail coverts and abdomen; chest and median portion of breast yellow. Outer webs of wing coverts and remiges partly yellow; inner webs of rectrices (except middle pair) with a subterminal white patch.

FOOD

Lawrence goldfinches eat mostly plant material. They search in flocks for patches of low herbaceous plants and shrubs that bear seeds. On the Hastings Reservation, compared with green-backed goldfinches, they eat seeds from fewer kinds of plants and they forage over a smaller variety of conditions. They concentrate in winter on chamise achenes, and in early summer they are closely restricted to patches of fiddleneck which furnishes most of the food taken through nesting. Two exceptional observations on food involved the eating of an egg of mourning dove and feeding on jumping galls.

James L. Ortega (1945) on June 1, 1944, saw a Lawrence goldfinch eating an egg of mourning dove. He noticed a female goldfinch in a gulch overgrown with weeds. It flew into the lower branch of a small oak tree and there ate something in the nest of a mourning dove. The observer approached to learn what was of so much interest to this bird. The nest held two eggs; one was whole and the other was punctured. The goldfinch was eating the contents of the egg. Mr. Ortega had watched many Lawrence goldfinches, but he had never before seen them feed on the eggs of any bird. In the area they were not so common as the green-backed goldfinch, but they were not scarce. It was not known how the egg of the dove was first punctured; whether it was pierced by the goldfinch is open to question. The puncture, however, was not large.

A. E. Culbertson (1946) reported an example of Lawrence goldfinches feeding on jumping galls. In the week beginning August 7, 1944, he watched a flock feeding on seed fleas, or jumping galls (*Neuroterus saltatorius*). Several valley oaks (*Quercus lobata*) in a yard, four miles north of Fresno, California, were heavily infested with this very small gall. The galls occur on the leaves, are spherical, and are about 1 millimeter in diameter. The

dry shell covering the gall is extremely thin. The jumping is caused by the rapid extension of the abdomen of the contained larva which strikes against the inner wall. The adult insect before emerging from the gall also causes it to bounce, in which case the motion is caused by the extension of the legs. When on the ground the active galls bounce in various directions, sometimes leaping as much as a centimeter in vertical distance. There is a sound made by the gall which is readily heard, particularly when one stands under an infested tree. This seems to be caused by the larva undergoing the same motion which causes it to bounce on the ground. The bouncing of the galls was first observed about August 1, and the goldfinches were also noticed at that time, but there was no particular association between them. When a flock of about thirty birds continued to appear every day, the birds were observed more closely at short range with field glasses. At almost any time of day the goldfinches were present picking up the galls from the ground and gleaning them from the leaves in the trees. Most of the feeding was done on the ground but when the birds were disturbed, they would fly into the trees and pick the galls from the leaves. There was no way of determining whether the movement, or the sound, of the galls was in any way concerned with the feeding. Supposedly these two factors would be of little concern to a predominantly seed-eating bird. Perhaps the galls were just juicy seeds to these birds. Examination of the droppings of the birds disclosed only gall "hulls," suggesting that the diet, for the time being, was exclusively of these insects. Goldfinches were present and actively feeding on the galls on August 26, the date of the last record.

FOODS OF THE LAWRENCE GOLDFINCH IDENTIFIED ON THE HASTINGS RESERVATION

Salix laevigata Bebb.—At 6:30 A.M. on June 11, 1945, a Lawrence goldfinch ate seeds of red willow near a spring.

Phoradendron villosum Nuttall.—In midmorning on November 24 three goldfinches ate berries of the common mistletoe.

Beta vulgaris Linnaeus.—In the morning of the last day of July, 1948, two Lawrence goldfinches in a garden ate the green leaves of chard.

Amaranthus albus Linnaeus.—On November 26, 1938, twenty goldfinches in a vineyard perched on grape stems and ate seeds of tumbleweed.

Amaranthus graecizans Linnaeus.—On November 26, 1938, twenty goldfinches in a vineyard perched on grape stems and ate seeds of prostrate amaranth.

Lepidium nitidum Nuttall.—For nearly a month after the middle of March, 1938, large numbers of Lawrence goldfinches along with several other kinds of seed-eating birds congregated to forage in a vineyard on a south-facing gentle slope. The other birds were green-backed goldfinches, house finches, juncos, and lark sparrows. Generally the Lawrence goldfinch was most numerous in the flocks. On March 23 there were at least 100, with as many or more on March 25. On March 30, between 3:00 and 4:00 P.M. the flock was larger than ever, possibly double the size of any previous one. There were more individuals of this species than of all others combined. On the evening of April 15 this bird was second in numbers in the flock with approximately 50 individuals.

At first the most conspicuous plants flowering in the area were red-maids. By the end of March other prominent annual plants bearing seeds were red-stem filaree, annual bluegrass, and common pepper-grass. The birds were mainly in patches of the latter, and they seemed to be taking its ripening seeds, but they also ate other plant material. On April 5 many goldfinches picked at the lower parts of pepper-grass plants, and at

many places the seed capsules were missing. This might have represented a specific choice for that food at that season, or it may have been merely a habit established by the flock of birds that congregated repeatedly to feed in the area. For more than a week practically all of the feeding by the birds was in one small area. The flock tended to disperse on warm days and to congregate on cold and cloudy days. Early in April some of the birds were attracted to other feeding grounds when the nutlets of fiddleneck began to mature. On April 15 the seeds of shepherd's purse were available in the vineyard and the birds then ate them also. The large size of the flock seemed to act powerfully to attract more birds and to cause a steady increase in size of the flock as long as other conditions remained favorable for foraging in the area. On rainy days the feeding was more general between showers.

Adenostoma fasciculatum Hooker and Arnott.—The abundant chamise provides food for this bird and several others from midsummer until late winter. The Lawrence goldfinches begin to eat the fruits while the bushes are still in flower. At 9:10 A.M. on January 20, 1938, at least one bird in a large flock of goldfinches ate chamise achenes. Three lit in the top of a small blue oak in chaparral. On January 25 one with a goldfinch flock ate chamise achenes in the same place.

A goldfinch eating achenes of chamise in the afternoon of a mid-February day perched about 3 inches from the end of a branch. It removed the achenes one at a time and swallowed after each peck. On a February morning a flock of six, along with a pine siskin and a green-backed goldfinch, ate chamise achenes at the edge of a patch. The observer could detect no differences among the bird species in the manner of taking the achenes. These they took from any part of the plant and by all sorts of bodily contortions. The Lawrence goldfinches flew away before the other two birds left. In the morning on February 7 at least one Lawrence goldfinch, with other goldfinches, ate chamise achenes. In early afternoon a week later at least six birds in a flock ate chamise achenes.

In the late afternoon of July 1, 1939, a goldfinch ate the maturing fruits of chamise along with several green-backed goldfinches. A pair on August 15 ate achenes of this plant. Manner of foraging in the bushes was watched for 10 minutes on a July morning. A family group of parents and two young, along with a single green-backed goldfinch, fed in three bushes in an area 12 feet across. The two adults spent the whole time on their respective perches in the highest branches 6 feet up and 8 feet apart, and they fed quietly and continuously, keeping the body upright and reaching upward and forward to the clusters of flowers and ripening achenes. The young birds fed themselves only two or three times in the 10 minutes. The birds stripped only the basal half of each spray; thus they took only the drier fruits and left the green ones.

At 7:15 A.M. on August 6 on top of a hill a flock, of about ten individuals, flew from the top of a 20-foot high valley oak and landed in a closely spaced stand of chamise, 80 feet to the south. Six minutes later the flock was still in the same bush, as individuals called and moved about. Three individuals fed in one bush about 5 feet high and the birds were 1 to 1½ feet below the top. They ate the flowers or the fruits. The adult male fed at the top of a bush 4 feet high; he dipped his head to feed 31 times in 35 seconds. The adult female and one juvenile fed at the top of a bush 4 feet high. The juvenile made 10 feeding motions in 30 seconds. Differences in feeding between this individual and the adult male were that the male lowered and raised his head rhythmically, whereas the juvenile paused at irregular intervals between feeding motions. The adult male did not appear to pull at the parts of the flower head on which it fed, whereas the young bird tugged at the flower head at each feeding motion. The flock was disturbed after 20 minutes by something unknown to the observer, and it flew downslope out of sight. Examination of the bush in which the female and the juvenile fed revealed many stripped flower heads. Beneath these heads, on the ground, were numerous flower parts. The plant was 76 inches tall. The birds fed on flower heads on the eastern side of the plant, and 73 inches aboveground. The plant was somewhat isolated from the main stand, being separated by a gap of 3 feet from its nearest neighbor. Early in a morning toward the end of September the Lawrence goldfinches seemed to forage more industriously than the green-backed ones. Late in the afternoon at the end of November at least two goldfinches fed on achenes of chamise along with other goldfinches at the edge of a patch along a fence. The group of birds kept together for 15 minutes and stayed in one or two bushes exposed to the sun even though thousands of other chamise bushes were available.

Rhamnus californica Eschscholtz.—In September, 1938, goldfinches joined flocks of Mexican bluebirds that visited coffeeberry bushes and ate ripe fruits. The goldfinches pecked into the sides of ripe berries and left the fruits attached. In the afternoon of October 5, 1939, five goldfinches in a coffeeberry bush ate the fruits.

Ceanothus ramulosus (Greene) Nuttall.—One of a group of four goldfinches, on the way to water, picked and ate a seed from coast ceanothus.

Clarkia elegans Douglas.—A goldfinch, in an early February afternoon, ate the seeds of canyon clarkia by pecking once at each capsule. It flew away after working two capsules.

Plagiobothrys nothofulvus (Gray).—On April 10, 1939, Lawrence goldfinches in a flock mixed with green-backed goldfinches fed on the ripening nutlets of rusty plagiobothrys in a remarkably thick stand on a south-facing grassy slope. The birds were closely restricted to this kind of plant, and they ate from no other.

Cryptantha muricata (Hooker and Arnott) Nelson and Macbride.—After midmorning of a cloudy day in early July, 1938, ten or more Lawrence goldfinches foraged, along with two or three green-backed goldfinches, at the base of a steep hill and close to a creek. The vegetation here had been burned a year earlier. The Lawrence goldfinches fed on the nutlets of the large prickly cryptantha that grew in patches on the barest parts of the washes at the base of the hill. Apparently they visited only this plant, which was then beginning to turn brown. The Lawrence goldfinches were not seen that day on any other kind of plant. The green-backed goldfinches were not seen on this plant, but at the same site those birds ate seeds of chia and Indian tobacco, mainly the former. This behavior shows the way in which the closely related species sometimes contrast sharply in habits, even though there is generally close resemblance in their behavior. Even in this example, the first impression was that of community feeding.

Amsinckia intermedia Fischer and Meyer.—This goldfinch has a special predilection for nutlets of the Boraginaceae. That family is represented by many (20) native species on the Reservation. Some of these, especially the common fiddleneck, grew abundantly in the deserted hayfields for several years after the Reservation was established. Those were the years when the Lawrence goldfinch was most abundant. When the patches of fiddleneck became smaller, the number of nesting goldfinches also became smaller. Continuous watching from early April to late July indicates greater dependence on this one food than on any other. Almost invariably a feeding goldfinch at that season is in a fiddleneck plant.

In early morning on April 11, 1938, in fog, several pairs, with green-backed goldfinches, picked out and ate nutlets of fiddlenecks on plants 2 to 3 feet high. On April 15, 1951, at 6:30 A.M. a pair of goldfinches lit on fiddleneck 8 to 10 inches off the ground. On April 16, 1938, most of the goldfinches ate nutlets where they were still green, but hard. The plants were too weak to support the birds which were usually carried down to the ground. On April 24, 1939, in the morning, a pair ate ripening nutlets. At the end of April a flock of twenty-five birds with a smaller number of green-backed goldfinches and a single house finch in a field from 8:30 to 9:30 fed on nutlets of fiddleneck. At intervals the whole flock would fly to some near-by tree. No sign of intolerance was detected, either while feeding or when perched in the trees, the birds sometimes being close together. The night had been cold and clear with temperatures below freezing.

Once, the Lawrence goldfinches eating fiddleneck fed outside the clump more than did a female green-backed goldfinch at the same place. She tended to stay inside the cover. They often fed head down and clinging to the top side of the spike. They were then taking nutlets from about 4 inches below the tip of the spike and just below the flowers. Two pairs did not feed as close to two green-backed goldfinches as to each other. At 5:43 P.M. on May 10, 1951, 3 males and a female fed on fiddleneck 8 inches from the ground and 2 feet from a fence. One male lit on an erect spike, 8 inches from the top, then moved his feet one by one 4 inches up the stem. The spike bent in a limber manner to support the bird.

On May 20, 1942, a male flew to fiddleneck and pecked among the flowers. The spike began to bend under the weight of the bird. Each time the bird pecked, the stalk not only bent down, but it began to roll under. Soon the bird hung upside down, pecked

sideways, and then it flew to another stalk. All of the spikes with flowers were about the same height, $2\frac{1}{2}$ feet. The female flew from the wire and lit by the male on the spike. The spike bent and both birds were forced to fly.

On May 23, 1942, a male and female fed on fiddleneck along a fence. They were at first in company with four green-backed goldfinches. When the green-backs flew off, the Lawrence goldfinches flew to a coffeeberry bush. They perched about 4 feet from the ground, the male on a twig 4 inches above and 6 inches away from the female. The male flew out over a field but the female did not follow. About 50 feet out the male turned back to its original perch. Goldfinches fed on fiddleneck in the afternoon. A pair beneath a 40-foot spreading valley oak fed for 6 minutes in an area 5 feet in diameter. The male stayed higher in the plants than did the female which was generally screened by the surrounding grasses. A pair foraged at the side of the road. They worked upward toward the top of a plant. In 3 minutes the female removed the fruits from 23 of the receptacles on one spike. The fruits were green but not yet ripe, for they were still green.

In midmorning on June 4, 1942, ten goldfinches, all Lawrence, half males, fed on fiddleneck, all in the same plant. There was some jostling as two birds landed on the same plant; some were upright, and others nearly inverted. On being disturbed, the flock "exploded," each bird rushing laterally 3 or 4 feet from the bush; then they closed in again to form a flock which flew to willows 20 yards away. The invasion of one field in large numbers by this species began on June 10 in 1946. After that date it was a common sight to see at least 75 goldfinches at fiddleneck stands. The flocks lit on the fiddleneck to feed on the still adherent fruits. In early morning in mid-June a flock of thirty goldfinches fed in fiddleneck. The next day more than fifty adults and young fed in the area.

The tendency to congregate in small space was demonstrated when foraging in the afternoon of June 26, 1938. About fifteen birds assembled, one or two at a time, in a small clump of fiddleneck and they fed at the same time in a space only about 3 feet across. When they left they flew off one or two at a time in different directions. Then seven, all that remained, flew off together. In less than a minute the birds began again to settle in another clump that was even smaller than the first one. Each bird began immediately to eat the seeds.

In early July, 1946, most of the fiddleneck in one patch had dried up, and only about 15 goldfinches were there. This was a considerable reduction from the size of the flocks that had been present the preceding month. On the afternoon of July 4, 1939, immature birds still ate nutlets 3 inches from the tip of the stem. On July 12, 1948, many ate seeds of fiddleneck, then dry and hard. They were mostly males and they permitted close approach by a man, sometimes within 3 or 4 feet.

A single goldfinch on July 22, 1948, fed on fiddleneck 2 feet high. The patch was in a grassy area and in the shade of a valley oak. For 5 minutes the bird clung to the small stems in the upper one-third of the plants and constantly flicked its wings at about half-second intervals, opening them only slightly, not to support itself in the air. The bird leaned forward and downward and picked the nutlets from the stalk near its feet. In August a Lawrence goldfinch with a flock of green-backed goldfinches tried to light on a stalk of fiddleneck. One observer heard the birds cracking the nutlets.

Trichostema lanceolatum Bentham.—At 7:35 A.M. on October 5, 1951, one goldfinch perched on a drying stalk of vinegarweed and extracted nutlets from the capsules.

Marrubium vulgare Linnaeus.—Horehound grows in large patches on open ground formerly cultivated in one canyon on the Reservation. This introduced mint provides nutlets that are eaten by goldfinches. Two goldfinches in early afternoon on October 19 perched on horehound plants and pecked at the heads.

On October 21, 1954, a flock of more than ten Lawrence goldfinches foraged in a dense clump of common horehound. As the observer approached five birds, they flew up from the vegetation and perched along the top wire of a fence. After 3 minutes the birds flew downward into the horehound. Others of the species joined them. Two perched 10 inches apart, obliquely on stems of horehound, about 8 inches above the ground. They each pecked at whorls of dry inflorescence, presumably for nutlets. Six birds in a patch were foraging. In the horehound they were so well hidden that it was difficult to see them.

Madia sativa Molina.—In early morning on August 1, 1948, a group of six goldfinches, including an adult male, fed on achenes of Chile tarweed left in the dry receptacles of dead plants.

Madia gracilis (Smith) Keck.—About 7:00 A.M. on June 9, 1939, a male goldfinch perched on a dead oat stem and pecked dry terminal achenes of gumweed. He did not eat the maturing fruits below this one.

Lagophylla ramosissima Nuttall.—In early morning at the end of June, 1938, a goldfinch, perched on a wire on a level with the flowering heads of a 2-foot tall slender rabbit-leaf plant, picked at the plant for several minutes evidently taking achenes from it. Also, the bird ate nutlets of fiddle-neck that it reached from the same wire. A goldfinch, with house finches, on July 27, 1941, ate achenes of slender rabbit-leaf. Early in the morning of August 1, 1946, an adult female and a young bird ate the achenes of slender rabbit-leaf.

Cirsium coulteri Harvey and Gray.—Early in the morning on August 11, 1946, two out of a group of four goldfinches flew to heads of thistle, picked achenes from them, and ate them while clinging to the plant.

Centaurea melitensis Linnaeus.—At noon in mid-February several goldfinches fed in a small patch of Napa thistle. They perched on the stalks near the heads and pecked down into them. Occasionally a bird broke off a head which it placed under a foot, held it down, and removed the achenes. On close approach the observer could see the birds drop pappus from the achenes before swallowing them. This session of feeding lasted for at least 15 minutes. Early in the morning on August 1, 1946, an adult female and a young bird ate the achenes from Napa thistle.

Eating salt.—The goldfinches regularly find sources of salt and they return repeatedly to supplies about saltlicks or other deposits on the ground. Two Lawrence goldfinches on the morning of February 20, 1938, visited a salt block at an old stock salting station on the Hastings Reservation, along with three house finches. At 9:30 A.M. on February 25, 1938, a male goldfinch, along with four or five house finches ate salt here. Again, on the morning of March 12 two females ate salt with house finches at the same site. At 8:00 A.M. on March 14 about twelve goldfinches were around this salt station with a few house finches.

Early in the morning on May 17, 1942, a pair of Lawrence goldfinches fed at the site of an old salt-block stand in a pasture. No salt block was present then, but the ground at the spot was bare, evidently because it had been penetrated by salt. Brome grass surrounded the area. The birds picked at the sandy ground as they moved over an area of less than a square yard. The male picked less than did the female, and he was disturbed by the observer standing 12 feet away.

Salt was offered continuously in a partly wooded pasture on the side of Mount Diablo, California (Peterson, 1942:73). A near-by water trough attracted seventy species of birds during the year. Four of these were seen to eat salt. Lawrence goldfinches picked at crystals occasionally, but most of their feeding was from the soil within a foot of the block. These birds came in flocks and covered the salt-saturated ground. Lawrence goldfinches used the salt through the nesting season, but by June even these birds stopped coming.

These observations show search for salt in winter and as late as mid-May. Where the hour of salt feeding was recorded, it was in the morning, the latest time was 9:30 A.M.

Eating sand.—In the late morning of May 23, 1942, a goldfinch flew down to a damp area of sand and gravel. It pecked at a small lump turned up by the observer's foot-step an hour earlier. The bird was tame and it permitted

the man to come within 6 feet of it as it picked off bits of the grit. More than forty pecks were counted. Examination of the sand showed bill marks, but there was no sign of seeds. Evidently the bird's sole aim was to pick up the gravel.

In early April, 1948, near Upper Lake, California, George L. Sherman (MS) saw five Lawrence goldfinches along with several green-backed goldfinches working on some waste sand and plaster 50 feet from a new house. The birds picked off particles of a new type of plaster.

USE OF WATER

At 5:45 A.M. on July 2 a group of five goldfinches made several trips to a creek. They drank at the margin and flew off with tinkling notes. From 5:00 to 5:30 P.M. on July 24, 1948, Lawrence goldfinches came in groups of five or six to drink at the overflow from a well beneath the shade of willows.

At 9:45 A.M. on August 2, 1946, four birds went to drink from a pool in a creek. The next day at 6:15 A.M. two goldfinches went to drink from the overflow below a tank. First, they perched for 15 seconds in a live oak, and they returned to the oak before leaving the site. Four hours later at the same place six birds came in search of water, but the stream had dried up, and they left after two birds pecked at the moist ground. In the morning of August 8 an observer saw eight goldfinches go to a creek to drink. At 6:30 A.M. on August 6, 1948, a group of seven goldfinches, including an adult male, drank at a water trough. At 6:00 A.M. on August 11 two goldfinches flew to low rocks in the center of a stream to drink. They then perched in low willow branches 2 feet above the water and a third bird flew to the rock to drink. A week later at 6:30 A.M. five goldfinches came to drink beneath the willows at the creek and at 9:30 at least six came to drink at the same place. They flew off after a stay of 3 minutes. At 10:45 A.M. on August 21 at least ten birds flew down to a pool to drink.

On the morning of August 22, 1949, a male goldfinch ventured down across the final 2 feet to a willow, landing 6 inches from the water, and hopping up to a tiny 10 x 12-inch pool $\frac{1}{2}$ -inch deep and out onto submerged twigs. He dipped his beak and tipped back fourteen times in rapid succession during a 20-second period. He was joined by first one bird and then the other of his contingent. When through drinking, he immediately flew 4 feet back up into the willow. When he was finishing, the second goldfinch dipped its beak once from outside the pool, but when the male had gone it moved onto a twig $\frac{1}{4}$ -inch below the water and drank eleven more times. Another dipped hesitantly twice, but he then waited until the first bird had finished and was gone before he returned to the water, and dipped ten times. All three then moved up through the willows and out of sight, making their faint tinkling as they left. In the next 5 minutes their procedure was followed closely by two more males, each of which approached along the same route and drank separately from the same pool.

At 11:00 A.M. on September 1, 1949, a group of at least sixteen goldfinches cautiously approached a water supply, moving in from willows farther downstream into the upper branches and dropping gradually from near the tops of the bare branches within 5 feet of the water. Only one of the sixteen

was an adult male. One other had poorly defined black areas above and below the bill, these coarsely intermingled with gray. Most of the birds were predominantly gray with but little yellow or dark coloration. Three bold individuals, the one obvious male not among them, led the movement to the water from branches 5 feet away, and within 3 minutes at least eleven of the birds came to the water and drank sparingly. One that the observer watched dipped only three times before flying at its own volition back up into the willows 12 feet above.

At 8:42 A.M. on September 23, 1953, a male and female goldfinch drank at a creek. They flew after about 1 minute. At 8:52 a male and female goldfinch drank at a creek. They flew after about 1 minute. At 8:52 a male and female worked their way through a red willow overhanging the creek, dropped to a branch about 2 feet above the creek, and flew down to the water and drank. They flew after 10 seconds. At 8:54 a female returned to the creek, drank for 30 seconds, and then flew away. Twice on mornings in the latter part of September, 1946, a single male flew down from willows and drank overflow from a well.

At 5:00 P.M. on October 12 a male drank seven times at the edge of a wooden trough. The next morning at about 9:00 A.M. three birds drank at a shaded spot along a creek; two stood on the edge of a rock and the third in a small trickle of water that wet his flanks. On the 14th four Lawrence goldfinches in company with about ten green-backed goldfinches bathed and drank from overflow water below a tank. The next day 5 minutes after fifteen green-backed goldfinches drank from the overflow late in the morning, a male Lawrence goldfinch came alone and drank for 35 seconds.

Manner of drinking was demonstrated by a pair perched on the edge of a water trough in midafternoon on October 19. The male flew to the opposite side and faced away from the water as he lit, but he instantly turned to face the water. The female followed within one second and lit $1\frac{1}{2}$ inches from the male. The male drank first, and then the female drank. A bird drank about once in each $1\frac{1}{2}$ seconds, with head and body down and tail up in order to put the bill in the water and head and body up with tail down in order to swallow and sometimes to glance around by turning the head. Up to the fifth drink the female always followed the male. On the sixth drink the female preceded the male. When the male flew off, the female drank once more; then she followed him to a tree.

At 2:00 P.M. on October 22, 1954, a flock of more than 20 Lawrence goldfinches came into a willow at the side of a water trough. They chattered their thin, plaintive notes for about 12 minutes as they moved about in the dead branches. Finally two came to the edge of the trough and drank. Immediately others descended also. There was great fluttering and flying back and forth between the two willows and the trough. At one time as many as twelve were lined up, six along the end-board. Five were on a floating board and one or two on the west side. As two or three left, others immediately took their places and drank. Each time one flew suddenly away, the entire group took flight. One group of eight left the topmost branches together; another group of six left together after they drank. At one time three males and two females perched on a tangle of dead twigs, 5 feet aboveground within a triangular area $18 \times 20 \times 6$ inches. The two females perched 2 inches apart

crosswise on the same $\frac{1}{8}$ -inch diameter twig. One male perched vertically on a twig 6 inches above them.

When one flock of eight birds took to the air, five were slightly more than a wing length apart, two were as close, but they were 2 feet behind the others. They flew outward 6 feet, then changed direction suddenly and all eight veered sharply to the left at an angle of 70° .

At 2:23 P.M. another flock arrived at the water trough. As four perched along the margin of the trough to drink, an acorn woodpecker (*Balanosphyra formicivora*) perched 20 feet above the ground in the top of a willow, gave its harsh 3-syllabled call. Instantly the goldfinches flew 15 feet into the willow foliage at the northeast end of the trough. At 2:30 P.M. eight birds perched in the topmost dead branches 18 to 22 feet aboveground; no two birds were closer than 5 inches. Two males and one female perched crosswise along a living $\frac{1}{4}$ -inch willow limb, evenly spaced, about 5 inches apart. Five were perched along the south end of the water trough when a golden-crowned sparrow flew to the margin to drink. One Lawrence goldfinch left; the golden-crown hopped 4 inches and took its place while a sixth Lawrence goldfinch arrived and moved into the midst of those that were drinking. This one perched so that its tail touched the water. Its head was directed away from the water. All the others drank. They lined up so close there were only $\frac{1}{2}$ - to $\frac{3}{4}$ -inch spaces between them. The golden-crown perched 2 inches from them. There was no disturbance. A group of seven came to the trough by short flights downward, stopping at three perches in 8 feet.

At 1:40 P.M. on October 23 a flock was at a water trough. Seven birds lined up along 18 inches of the southeast end-board and drank. When a Lawrence goldfinch flew downward from a willow at the northeast end of the trough, it perched facing southwest and had to turn around to drink. When the birds flew to the trough from the southeast, they perched directly and drank. One male drank three times, two other males four times. No more than seven were lined up at one time. Each time another goldfinch joined or attempted to join them, one that perched immediately flew away. Only once did a newcomer take the perching place of the one that had flown.

At 2:00 P.M. two green-backed goldfinches and one male Lawrence goldfinch perched at the edge of the water trough. This male lowered his beak into the water 10 times in 15 seconds. An Oregon junco arrived and perched within 2 inches of the Lawrence goldfinch. Immediately the latter flew. At 2:10 P.M. one female and one male Lawrence goldfinch perched between two Oregon juncos to drink. The male Lawrence was the last of the group to arrive. It chose a spot beside the female within 4 inches of one of the juncos, although all the rest of the water trough margin was available.

Three Lawrence goldfinches along with ten green-backed goldfinches at 10:00 A.M. on October 27 flew down to a creek to drink and bathe. Mexican bluebirds and cedar waxwings bathed at the same place, and all four species remained within a small area with no sign of intolerance from any toward another. At 10:30 A.M. on November 23, 1937, two birds drank at a water trough.

In the morning on April 9, 1939, three or four goldfinches preened after bathing at the lower end of a running stream. A female moved to a perch close to a male while preening and then shifted so as to be beside another male

perched 10 feet away. Neither male seemed to pay much attention to the female, only 2 or 3 inches away. At 5:00 P.M. on April 20, 1938, two goldfinches bathed in a creek and dried their plumage in a locust tree and rose bushes.

At 2:00 P.M. in mid-May three goldfinches at a pool in a creek bathed along with mourning doves, Mexican bluebirds, and house finches. We recorded goldfinches bathing in a creek on an afternoon in early June. A pair in early morning on June 8 bathed in a creek. At 6:40 A.M. on June 9, 1946, even though the pool was in shade, the early morning fog was only beginning to break, and the air was moist and cool, two males and two females lit on the sand at the edge of the pool and spent 40 seconds drinking. At 5:45 A.M. on June 16 birds bathed in the shallow margins of a creek and then flew up to wires where they preened and dried their plumage as they sat in the sun with feathers fluffed.

At 4:00 P.M. on April 27, 1949, a male was drinking from a drain at the corner of a house. This was the first member of the species seen for three weeks.

PERCHING

Lawrence goldfinches characteristically perch high in the crown of any tree they land in and they remain on the twigs and small branches just inside the leafy canopy. At these sites they twitter and call in a high, thin voice.

On a morning in late July, 1950, a male perched on a newly installed electric power line. The site was 100 feet from a large valley oak. The bird remained for 3 minutes, occasionally turning 180°; then it descended to a patch of fiddleneck. In midmorning on April 2, 1938, first a male sang in the top of a slender blue oak; then a female came to the same tree, and a few minutes later a third bird arrived.

PREENING

At 10:00 A.M. on May 27, 1939, a female goldfinch preened on the nest. She stretched her left wing and kept on preening, especially on the breast. The male sang 15 feet north of the nest, but the female paid no attention to him and kept on preening. Preening by the female may substitute for the exercise lost because of reduced flying. These birds seem to preen more than the other passerine birds studied in the area, but they stay on the nest much more than the others. The nest is well-concealed so that considerable motion is permitted without the female being conspicuous.

At 5:14 A.M. on June 9, 1939, a female vigorously preened and scratched in the nest. This was an almost continuous process from the time she returned to the nest at 5:20 until 6:26. Something on the left occipital region required vigorous scratching at intervals of not more than 10 minutes.

At 10:00 A.M. on October 18, 1939, a male and three females preened in big willows. The trees made a windbreak against the west wind.

ROOSTING

In January and February, 1928, Frank F. Gander (1930:64) observed that small flocks of Lawrence goldfinches numbering from eight to twenty

were common about his home on the outskirts of San Diego, California. The birds fed daily on the achenes of chamise. Some fifty, or more, roosted nightly in a large clump of lemonadeberry (*Rhus integrifolia*) in the center of a grassy patch in a canyon. On several occasions at dusk and at dawn the birds were flushed from this bush. In the first two months of 1929, however, not even one Lawrence goldfinch was seen in that neighborhood.

SUNNING

In the afternoon on March 27, 1938, the goldfinches in an oak tree mostly preened on the sunny side of the tree. In early afternoon in the first part of April, 1938, several goldfinches were in a poison oak and rose thicket beside a creek, preening and singing in the sun after bathing, along with lark sparrows. This was a resting period after foraging. A male and female on a telephone wire in early morning in mid-June ruffled their feathers and sunned themselves, but they did not join a flock that flew near by. We often see groups of Lawrence goldfinches sunning themselves in the top of a tree. At 6:45 A.M. on August 23 three birds sunned in the top of a dead, white alder beside a creek. After 10 minutes they flew downstream. At 6:40 A.M. on August 26 six birds perched in the same tree. Occasionally one preened, but for the most part they sat simply sunning. After 12 minutes the birds flew away, but at 6:56 six more were back in the tree. On August 29 at 7:15 A.M. at least thirteen goldfinches perched in the top of this dead tree. At 6:45 A.M. on August 26, 1949, three goldfinches perched in the early morning sun close to the top of a tall red willow. Faint tinkling sounds came from others deeper in the willows. At 6:50 A.M. on October 2, 1944, four goldfinches perched quietly on twigs at the top of a 15-foot willow beside a creek. They sunned themselves and made no move or sound.

FLOCKING

Early in the morning of June 20, 1948, a flock of sixteen goldfinches flew across a narrow field from a patch of fiddleneck toward a willow. On rising they gained altitude to 30 or 40 feet in the first 75 feet and then drifted down toward the upper part of the willow. The arrangement in the flock was loose, twisting, and milling, with the birds spread out 2 to 10 feet apart. There were only two or three adult males, but there were many dull-colored young of the year. These were as good fliers as the adults. Another feeding flock, two days later, contained thirty-one goldfinches, including many young birds.

In the morning on October 5, 1940, about fifty goldfinches in a flock in willows close to the lower end of a running section of a stream mainly perched within the canopy of the tree and all of them sang together in a chorus. In midmorning on October 17 eleven goldfinches on a telephone wire perched with an average space of less than 2 inches between individuals. They simultaneously flew about 30 feet to the ground where they foraged. On October 22, 1939, at midmorning a flock of twenty-five drank at the junction of two creeks. They flew from willow thickets 4 feet away, alighting on sunlit rocks in midstream. They were exceptionally nervous and flew up to

the same thickets repeatedly. They went down to cluster around the first bold individuals, as if requiring a nucleus.

At noon in the third week of May, four or five pairs fed together on fiddleneck. Superficially, they appeared to make a flock, but they kept obviously in pairs, both when disturbed and when dropping back to the plants to feed. When feeding, and in the plants when disturbed, pairs often intermingled temporarily, but it was easy to distinguish the pairs. Occasionally, two or three of the males sang quite typically.

At 8:30 A.M. on March 23, 1939, two flocks were at the lower part of a vineyard. The fifty birds were near the ground and in a tall blue oak. In the afternoon of March 26, 1938, the flock that congregated in a vineyard contained more birds than on previous days. Between 3:00 and 4:00 on March 30 it was nearly double the size of the flocks seen in the same area on previous days. In the evening on April 12, just before a rain, the flock of goldfinches was larger than had been present there for several days, and the organization of the flock was by pairs.

At 8:30 A.M. on June 21, 1941, a flock of five males perched along a fence wire. No female was seen that day. On April 1, 1948, a group of four goldfinches along a road were all males. These were the first members of the species observed in several months.

In early summer groups of males tend to form flocks. At 5:30 P.M. on June 20, 1942, about fifteen goldfinches with two house finches made up a flock. These flocks occur while the females are almost continuously on the nest and before the young birds are able to fly. One male flock was foraging in fiddleneck at 6:00 A.M. on June 22, 1941.

In the afternoon of June 22, 1952, 75 to 100 goldfinches assembled to forage on fiddleneck in an open area. One group of fifteen birds occupied a patch of fiddleneck 8 feet across. The birds shifted from one stem to another, singly or in groups. The flocking tendency was pronounced. The sudden flight of a small group of California quail caused the flock of goldfinches to move to the willows and other trees bordering a creek. The goldfinches perched 3 to 10 feet above the ground on the outer branches of the trees. Within 2 or 3 minutes most of the flock returned to forage in the field.

In the morning on September 15, 1938, a small flock of goldfinches foraged in chamisal. When the birds were disturbed, they flew to higher perches, in blue oak trees, but soon they returned to the abundant achenes.

ASSOCIATION WITH OTHER BIRDS

Accipiter striatus Vieillot.—At the end of June, 1938, remains of a Lawrence goldfinch on a log on a wooded hill indicated that one had been eaten by an accipitrine hawk. The many newly grown feathers were those of a young bird.

An observer watched the near capture of a goldfinch by a sharp-shinned hawk in the early afternoon on June 14, 1946. The hawk flew out of creekside vegetation and dived into a flock of about thirty-five goldfinches feeding on fiddleneck in an open field. The approach of the hawk was so swift and it came so silently that it covered the 30 feet to the finches and started a dive from 15 feet above the flock before the birds took alarm. The bird at which the hawk aimed was approximately in the center of the flock. It flew up when the hawk was not more than a foot away. The rest of the flock took alarm simultaneously. The hawk veered up in pursuit, and the momentum from its downward plunge was sufficient for it to overtake the goldfinch. But at that moment the finch must

have made a quick maneuver in another direction, for the hawk failed to get it. The hawk immediately returned to the thicket along the creek. By that time the flock had dispersed and the birds had reached cover on the creek.

On July 14, 1939, at 8:39 A.M. a sharp-shinned hawk flew to a valley oak and perched on a limb in clear sight of the Lawrence goldfinch's nest. Two Bewick wrens began to chatter. The young goldfinches had actively preened and moved about, but they froze into a rigid position on the nest rim. The adults did not show up. At 8:45 the hawk flew away. Two minutes later one of the young goldfinches climbed an upright limb for 3 inches. At 8:56 the young were on the rim of the nest again. At 9:05 the adults flew to a valley oak across the ravine and the young began calling. At 10:10 A.M. a sharp-shinned hawk flew to a live oak near by a ravine, and the goldfinches stopped calling. The male perched on the top branch; it looked about, especially in the direction of the live oak. The female perched near and above the nest and called *way* softly. The young crouched low in the nest.

Lophortyx californica (Shaw and Nodder).—Six goldfinches fed in a patch of fiddle-neck on May 14, 1939. Two flew away when a pair of California quail flew into near-by willows. The other four were closer to the quail, but they did not fly. At 10:15 A.M. on September 7, 1939, the singing of goldfinches was silenced twice for periods of 35 and 25 seconds by warning clicks of quail below them. As soon as the quail had flown away, the goldfinches resumed their singing in spite of an observer's continued presence.

Calypte anna (Lesson).—When a young Lawrence goldfinch only a few days out of the nest, in May, perched near an Anna hummingbird's nest, the owner of the nest tried to drive it away. The goldfinch dodged and shifted its position, but it did not leave immediately. An incubating female flew off the nest and perched 12 feet away in another tree. This was 4 feet from a nest of an Anna hummingbird. The hummer flew off the nest and hovered in front of the goldfinch, inspecting her but not making loud hums. The goldfinch hopped toward the hummer which backed off and returned to her nest.

Sayornis nigricans (Swainson).—In late June a male black phoebe drove away a house wren from the vicinity of the phoebe's nest where the eggs were hatching, and then it flew to a fence 25 feet from the nest. A few seconds later a male Lawrence goldfinch lit 9 feet from the phoebe. There was no indication of conflict between these birds, and they flew off in opposite directions in less than a minute.

Myiochanes richardsonii (Swainson).—At 6:33 A.M. on May 26, 1940, a female wood pewee chased a male goldfinch from a branch 20 feet west northwest of a pewee nest. He flew east northeast to a live oak and looked back at the pewee, which did not chase him. At 10:38 A.M. the male pewee chased a male goldfinch from the pewee nest limb 30 feet northeast to a lichen-hung willow. At 8:56 A.M. on June 12, 1940, a pair of goldfinches lit in willows 24 feet aboveground and 6 feet north of a nest of a wood pewee at a creek crossing. The male pewee foraged 5 yards north of the nest and failed to disturb either goldfinch. The female pewee, however, appeared and attacked one of the goldfinches, chasing it and snapping the bill for 3 or 4 feet. The goldfinch flew 15 yards up the creek to the north and out of view. The male then attacked the remaining goldfinch, but the latter apparently successfully resisted the attack, for the male pewee left the vicinity and the goldfinch continued to perch for 20 to 30 seconds within 6 feet of the pewee's nest. Then it left to fly up creek to the north in the same direction as that taken by the other member of the pair.

Aphelocoma coerulescens (Bosc).—At 6:10 A.M. on July 11, 1939, a scrub jay caused a disturbance at a goldfinch's nest. The adult goldfinches flew to a blue oak 40 feet east of the nest-tree where the female gave the *sweet* call and the male tinkled. They remained 30 seconds and then a scrub jay flew west from a blue oak 25 feet east of the nest with the goldfinches following it, one of them tinkling and the other giving a single-noted call every second. Another jay followed the goldfinches which flew among trees 100 yards west where the jays could be heard calling. At 11:45 A.M. on August 22, 1949, a little group of goldfinches was twice driven back into the dense willows by the sound made by a scrub jay which passed through a large red willow.

Parus inornatus Gambel.—When two Lawrence goldfinches on April 14 came within 10 feet of a plain titmouse nest in a sycamore, one of the titmice chased them out of the tree. On a June morning an incubating female was quiet on her nest until two titmice

began to forage 4 feet above her in the tree. She turned her head so as to look up with the right eye, but she was not alarmed and made no attempt to drive the two birds away. They moved on to another tree 8 feet away. Later in the morning a titmouse foraged within a foot of the goldfinch on the nest. She watched it quietly, but made no threatening gesture and did not try to drive it away.

Chamaea fasciata (Gambel).—In the morning of May 15, 1939, a male Lawrence goldfinch chased a male wren-tit out of some dense bushes beside a creek. This goldfinch had been seen there several times, and once a female came from the same location. There may have been a goldfinch's nest near by.

Troglodytes aedon Vieillot.—At a nearly completed nest at 8:52 A.M. on May 20 the female Lawrence goldfinch chased a house wren from the site in a blue oak, but the male took no notice of the intruder. On June 7 an incubating female in midmorning drove away a house wren from the near vicinity of her nest.

Sialia mexicana Swainson.—On the morning of September 8, 1938, several Lawrence goldfinches perched with Mexican bluebirds on a telephone wire along a lane. Others were on the ground near by in stubble. Through the rest of the month these two species were together regularly in visits to coffeeberry bushes where they ate the ripe fruits. On October 25, 1939, at 3:00 P.M. a male and female goldfinch bathed with bluebirds in a sunlit water trough. On November 24, 1937, at 9:00 A.M. three goldfinches ate mistletoe berries with bluebirds in a small blue oak.

Polioptila caerulea (Linnaeus).—A goldfinch in a flock on the afternoon of June 29, 1938, came near a blue-gray gnatcatcher's nest. The female gnatcatcher drove the intruder from the vicinity.

Dendroica nigrescens (J. K. Townsend).—Once in August when a black-throated gray warbler that was working through a tree in which a male goldfinch perched, came within a foot of that bird, neither paid attention to the other.

Passerina amoena (Say).—A fight between a male goldfinch and a male lazuli bunting took place at 6:00 A.M. on June 22, 1939, about 50 feet from the goldfinch's nest. The goldfinch was on his way to feed a female on a nest. He pursued, and fought with, the bunting and fell with it for 25 feet. The goldfinch followed the bunting into a bush, and obviously he won, but he left the vicinity. Later, the bunting sang in the top of the tree.

In midmorning the next day when the male goldfinch perched 30 inches from the nest, the lazuli bunting flew to a perch 4 feet from the nest. The goldfinch watched the bunting which looked at the nest and the goldfinch. When the bunting flew away, the goldfinch was startled, but he made no effort to drive away the intruder. This was the same bird he had fought the preceding day.

At 9:13 A.M. on July 14, 1939, the adults returned to the nest-tree and the male went to the northeast rim to feed the young birds when a lazuli bunting alighted 1 foot south of, and 6 inches below, the nest. The female goldfinch chased it around a live oak 20 feet and then returned to the tree. The male goldfinch had left the young and perched in a blue oak 20 feet southeast of the nest. The female joined him at the blue oak. The bunting returned at 9:14 and drove the male goldfinch from the blue oak to another blue oak 50 feet east of the nest. At 9:16 the male bunting chased the male goldfinch again to the northwest, circling over the ravine. The young goldfinches were still in the nest.

Carpodacus mexicanus (P. L. S. Müller).—On April 21, 1938, two goldfinches were present along the northeast side of a vineyard with a large flock of house finches and lark sparrows. A male goldfinch perched on May 21 in a dead-topped willow was displaced by a house finch in a manner that indicated intention to drive away the first bird.

Lawrence goldfinches often join flocks of house finches. Toward the end of May, 1938, about five goldfinches in a flock of more than thirty house finches flushed from an open, south-facing, grassy area. On June 27 there were five in a flock of house finches. The next morning at 7:20 about ten goldfinches were in a flock of house finches and on the third morning the same number foraged in a stubble field with about forty house finches. On June 8, 1941, pairs of goldfinches along a fence at the edge of an oat field were close to house finches which ate oat seeds. All through July, 1938, Lawrence goldfinches were a regular part of the flocks of house finches that foraged in the more open ground. Ordinarily, there were five to ten goldfinches in a flock of forty or fifty house

finches, but as many as twenty of the former were seen, and once that species outnumbered the house finches in the ratio of fifteen to ten. Once there were also lark sparrows in the flock.

At 4:00 P.M. on October 4, 1939, three males and one female perched on a fence with a flock of house finches. At 8:30 A.M. on October 13, 1939, in a pasture, eight goldfinches foraged on a shaded patch of dew-wetted green grass along with more than twenty house finches. When something disturbed the birds, all the house finches flew into an adjacent elderberry bush, but generally one or two goldfinches remained on the ground. A male goldfinch jumped 3 inches out of the way when a male house finch came down on top of him. On November 18, 1938, four or five goldfinches were in a larger flock of house finches on a fence and at a water trough near a barn.

Spinus tristis (Linnaeus).—In afternoon on November 8, 1939, one pair of Lawrence goldfinches with ten American goldfinches came to drink at a creek where the bank made shade.

Spinus psaltria (Say).—On July 14, 1939, at midmorning a female green-backed goldfinch arrived from the southeast at a Lawrence goldfinch nest-tree, perched at the north side of the tree, wiped off her bill on the second perch, and then flew to a live oak 15 feet north of the nest and disappeared into the canopy. She called three times *way, way*. At 10:30 A.M. an adult female green-backed goldfinch perched at the top branch of a Lawrence goldfinch nest-tree and called. A young bird flew to a branch 4 feet below her and preened its feathers before it flew away. At 10:20 A.M. on October 12, 1939, one male drank with fourteen green-backed goldfinches at a creek. It left with four of the latter. One male with green-backed goldfinches drank at a water tank overflow. Lawrence goldfinches often attach themselves to groups of green-backed goldfinches, because of their gregarious nature and the scarcity of their own species. There is no difference in the way they are treated by the green-backs.

Pipilo fuscus Swainson.—When a pair of goldfinches visited their nest around 9:00 A.M. on May 19, they were especially excited on perches 2 or 3 feet away while a brown towhee was at the nest.

Chondestes grammacus (Say).—In late afternoon on July 8, 1942, ten or fifteen goldfinches were feeding in company with six lark sparrows in an open area. The goldfinches were both male and female. They ate the ripe nutlets of fiddle-neck.

Junco Oregonus (J. K. Townsend).—In late March five goldfinches fed on the ground within 10 feet of a flock of Oregon juncos.

VOICE

Ridgway (1877:463) reported that this bird "uttered very pleasing and quite peculiar notes." According to Allen (1937) the songs of this goldfinch are lower in pitch and somewhat rougher than the songs of the other species, and it has among its call notes a harsh *kee-errr* that is quite different from the notes of the others. J. Grinnell (1912:106) noted several pairs in early May at Glendora, California, "with their wheezy notes." Grinnell and Storer (1924:436) characterized the song of the male as weak but varied and distinctive, and the call notes single, low, and with a tinkling quality. They pointed out that the song and call notes were so distinctive as to provide, after once learned, the readiest means of identification.

In the stages of nest building the normal song is more continuous and less strident than in many other small passerine birds. The song is mainly uttered when the male is close to the female, and its main function appears to be to maintain the attachment between members of the pair. It is also uttered when a male attacks a male, but the tone is not changed, as it is in some other species. When the male courts a female, the song is uttered in richer tone.

Many of the goldfinches in a flock on March 17, 1939, were singing in the tops of locust trees. On April 12, 1951, a male goldfinch twittered in the top of a locust in the early morning, the first of its kind seen that spring. Birds in a flock in late April moved actively among the branches of locust trees. They kept up a nearly continuous twitter that was varied and musical with thin, clear notes mostly high in pitch. On May 10, 1951, at 5:30 P.M., a male goldfinch was singing its high clear melodious song with many clear notes. On June 14, 1946, the twittering songs of many goldfinches in the willows was the dominant bird sound of a section of one creek.

At 4:47 P.M. on July 10, 1939, adult goldfinches flew to a live oak 30 feet from a nest and remained there 1 minute while the male called faintly and the female used the *sweet* call. The young were calling loudly. At 5:15 A.M. on July 11 one of two young goldfinches in a nest was giving the *sweet* call. No adults were visible. At 8:30 a male and a female flew to a nest-tree from a valley oak 2 seconds after one of the adults began the *tinkle* song. This flight song also seems to be the signal to begin flying. It is often noticed after feeding the young. At 5:26 A.M. on July 14 the young began *sweet* and *chee-up* calls. At 8:30 A.M. a male goldfinch was heard in full song by a creek. An observer heard the *whee* of a female goldfinch at 12:40 P.M., but it gradually diminished in volume as if the singer progressed up a slope. At 12:42 the adults flew to a blue oak 40 feet east of the nest and called. There was a weak *sweet* from the young. At 10:30 A.M. on July 28 in a large sycamore two goldfinches were present for about 3 minutes. One juvenile repeated a single nasal *churr* as it followed and perched near the adult.

At 6:15 A.M. on August 1, 1946, a female and a young bird were feeding, but both were silent except for small *tsip-tsip* calls made by at least one while foraging. On August 22, 1949, a group of three Lawrence goldfinches was in a willow above a small trickle of water. As they moved about they gave a faint tinkling note, reminiscent of glass wind chimes and differing markedly from the slightly louder metallic clanking voice of the green-backed goldfinches.

At 11:00 A.M. on September 1, 1949, sixteen goldfinches were observed on willow branches about $\frac{1}{4}$ inch over a stream. Faint tinkling sounds could be heard from the birds during the cautious approach and hasty departure to places 100 feet downstream. At 11:40 A.M. tinkling sounds continued from the same birds in the willows downstream. One unseen bird sang almost continuously for 5 minutes in a high pitched, rapidly moving trill, broken by a great many longer notes, a few of which demonstrated the finch-like slur. At times notes came so fast as to sound like two birds singing. At 10:15 A.M. on September 7, 1949, goldfinches sang and moved about in the leafy crowns of red willows. The song was a high-pitched series of trickling ascending and descending trills, chirrs and stuttering notes. Usually only one bird sang but occasionally one or more joined it, in which case the sounds became so mixed as to make it impossible to decide how many birds were singing. The song was higher pitched and weaker in volume than that of the green-backed goldfinch. The birds remained concealed while singing, but they were high in the tree.

At 1:30 P.M. on October 18, 1939, one male and two females were in willows; the male frequently calling with a bell-like note until he found the

females. At 4:45 P.M. a goldfinch called three times with clear, bell-like notes and the response was that a female flew across to his tree from 5 feet away. She did not answer him, but he flew to a perch above her. At 2:00 P.M. on October 22 a male goldfinch drank at an overflow from a well and called for his companion, using the bell-like *klee* and also a short pi-bi-di-dee-o. These failed to locate the desired bird, so the male left the vicinity, moving down the creek and calling from time to time. At 9:00 A.M. on November 1 a male was calling the "lost" note at a water barrel. At 2:00 P.M. the male was "lost" again. On November 18 a male was calling his mate, which he failed to locate; he sang three times at water. These were the first songs heard since the nesting season. At 3:45 P.M. on November 22, 1937, Lawrence goldfinches sang several times. For some time on December 19 at least two goldfinches were in the vicinity of a water barrel, where the male often called a lost female. The males of this species seem to get more excited over losing a female, and they lose the female often.

At 11:00 A.M. on February 5, 1938, two males sang in the top of a locust tree. At the same hour on February 25 a male sang in a willow beside a creek. In the evening on March 12, 1938, three goldfinches sang in the top of a locust tree. At 10:00 A.M. on May 7, 1940, a male lit in the top of a dead willow beside a creek. The bird sang three or four times and then flew off toward a hill. Early in the afternoon a singing group of about ten birds occupied a small locust tree. On May 19, 1939, a nest that had been built earlier in the spring was deserted. At 10:45 A.M. a male preened and sang on a perch 10 feet above the nest. At about 5:30 P.M. on May 27, 1939, where a nest was watched, several males began to sing: one was southeast of the nest, one was north of the nest, and one was east of it. All these birds were at least 100 feet away from the nest. The next morning at 4:36 A.M. the female was on the nest. Numerous goldfinches sang from the northeast to the south of the nest, but none was heard toward the west, where the trees were not inhabited by goldfinches.

FIELD MARKS

A Lawrence goldfinch is half the size of a junco. Plumage is gray-appearing; yellow on under surface is restricted to breast; outer surface of wing is marked with yellow. The male is recognized by the arrangement of the black about the base of the bill. The flesh colored bill as he faces an observer is encircled by black giving a hooded appearance. Wing and tail feathers are chiefly black, the former showing yellow and the latter white in flight. The black about the bill shows even in the winter plumage. The general color of the female is grayish brown. The white markings of the male are dully represented.

ENEMIES

The flocking habit of Lawrence goldfinches makes them likely prey for predatory birds. Sharp-shinned and Cooper hawks occur frequently where the goldfinches live. Pursuits are often seen, but the goldfinches nearly always escape. Scrub jays threaten goldfinches, especially in the nesting season, and they are generally on the look out for nests that are vulnerable

for destruction. Once in midmorning, in July, a fence lizard (*Sceloporus occidentalis*) climbed up the nest limb of a pair of Lawrence goldfinches and up the side of the nest. The lizard paused at the rim, looked into the nest, and turned back to retrace its path back down the limb. A crippled male goldfinch with an injured wing, probably broken by flying into a wire, fell helpless to the ground in a lane.

BEHAVIOR IN WINTER

Miss Emily Smith has observed (MS) that Lawrence goldfinches only occasionally winter in the Santa Clara Valley. On January 8, 1948, near Los Gatos a flock contained about twenty singing birds. At 8:45 A.M. on January 29, 1945, three goldfinches perched on crown twigs of a 20-foot leafless blue oak on a wooded slope. Two preened, had the feathers fluffed out, and were silent. The other one was singing a canary-like song almost continuously. The first Lawrence goldfinch found on the Reservation in the winter of 1950-51 was present on January 30. One in dull plumage fed steadily at heads of chamise in the brush on the lower south face of an open hill. After 8 minutes, at some alarm, the bird dropped down into the brush. Presently it flew off toward a wooded hill uttering occasionally musical *ter-week* notes. Farther down the ridge two of these dull-plumaged birds fed at the heads of chamise. One bird several times allowed the observer to come up 4 to 6 feet away. He could see its bill working each time after it picked off a part of the head. Evidently the bird hulled the achenes which it swallowed as soon as each was cleaned. At 1:45 P.M. on February 20, 1945, one lone male sang from a twig 10 feet aboveground at the interior of a leafless willow. He sang almost continuously. About 15 seconds after the observer saw the goldfinch, ten lark sparrows flew to the same willow and sang. In the confusion of their arrival the observer lost track of the goldfinch and did not see it again.

In some winters Lawrence goldfinches tend to move south and eastward through Arizona, New Mexico, and Texas. Winter status of the birds in recent years is indicated by the evidence summarized here from Audubon Field Notes.

On March 2, 1949, a small flock was seen on the Bosque Refuge, New Mexico. This was rather surprising since none was seen all winter in eastern or central Arizona (Monson, 1949). Large flocks fed and sang in the walnut groves of Hemet on February 11 (Stager, 1949).

Monson (1951) reported a flight of Lawrence goldfinches southeastward from their summer range in the fall of 1950. They were common at Tucson, and the species was present on November 30 at Tumacacori National Monument, Arizona. The birds were present at El Paso after November 16, including a flock of 42 at Ascarate Lake on December 2. In late winter (Monson, 1951a) this bird was common in lowland areas, including the Rio Grande Valley from Las Cruces, New Mexico, to Fabens, the last ones being seen at El Paso on March 20. That was the third year in 20 they had visited the Rio Grande. Large flocks were seen about Tucson, and a flock of at least 100 was noted in Tempe, March 25. They were even seen at Snowflake: 14 from February 11 to 17.

On the 51st Christmas Bird Count in December 1950, the highest count for the Lawrence goldfinch was 351, at Tucson, Arizona.

In the early winter of 1951 the Lawrence goldfinches made another eastward flight: about 20 were noted at Tucson on November 4, they were common at Liberty, Arizona, on November 12, and they were noted on the Colorado River Indian Reservation on November 9 (Monson, 1952:33). In southern California a flock of 75 Lawrence goldfinches near Lakeside on October 30 was still there on December 6 (Small and Pyle, 1952:39). The largest count for this bird on the 52nd Christmas Bird Count was 53 at Tucson. Later in the winter the goldfinches were scarce at Tucson with the last one seen on February 6 (Monson, 1952a).

In 1953 a flight of this species to central and southern Arizona developed with records after October 3 at Tucson, Peoria, Wikieup, Hereford, and in Sonora (Monson, 1954:35). In 1953-54 more than 50 Lawrence goldfinches wintered in the El Paso Area, nearly 170 were seen at Tucson, January 2, and more than 23 were still present at Tempe, March 17 (Monson, 1954a). In the spring these birds were widely reported in southern California: Imperial Valley (70) March 11, Whittier (25) February 6, and Indio (110) March 21 (Small, 1954).

SUMMARY

The green-backed and the Lawrence goldfinches reveal close resemblances in their behavior. These bring them together in common flocks. Under some circumstances they also accept other related birds, for example, house finches. They seldom challenge larger birds. The green-backed goldfinch occupies greater area than the Lawrence goldfinch in California, and the population of the former species is greater. The Lawrence is found in hotter, drier parts of California than the green-backs. Southward from Los Angeles it is a bird of foothills or mountain valleys.

Habitat conditions suited to these goldfinches are found on warm slopes, especially ones that face the southeast where warmth is available at nesting time. For perching and roosting they occupy trees with dense foliage. Trees in scrubby woodland with heavy festoons of lichens are suitable for nesting sites. Low bushes and tall herbaceous plants provide much of the food eaten by goldfinches.

Creeks, or some other reliable source of water, where the birds can drink and bathe as well as obtain moisture to soften the dry, hard fruits that make up most of their food, are necessary. Additional requirements are for thickets that afford escape from hawks, jays and other predators.

Pairing in these goldfinches occurs when the birds are in flocks. Courtship involves song and flight display. Males make high circular flights with wings and tails widely spread, revealing fully the courtship markings. The green-backed goldfinch has a long nesting season which extends from early March to July and, exceptionally, into November. The Lawrence occurs in variable numbers from year to year and it occupies a more restricted nesting area which tends to be concentrated southward. In winter this bird migrates toward the southeast.

In the spring of some years the goldfinches congregate in large flocks with

other seed-eating birds and forage on the seeds produced by the abundant plants that grow on open land that slopes toward the south.

Nesting on the Reservation extends from May to July for the Lawrence goldfinch and for a longer period in the case of the green-backed goldfinch. The female does most of the nest building, but the male remains close by and sings. Some males carry small amounts of material and they are attracted to the nest site in its early stages. Frequently a member of a nesting pair will drive off a strange goldfinch. The female may pursue other females and sometimes strange males. The nesting pair tends to ignore the presence near the nest of the green-backed goldfinch. The incubating female in both species remains on the nest almost continuously. She may leave after some feedings by the male. The male brings food (moistened paste from seeds) about once each hour. After the young hatch the female broods the nestlings for about 4 days before she begins to accompany the male to get food.

The green-backed and Lawrence goldfinches tend to forage together. The green-backs favor open pastures where Napa thistle grows. This plant is especially adapted to the needs of finches. Weed seeds provide the bulk of the food of these birds. The animal food reported from stomachs was mainly plant lice. On the Hastings Reservation we have watched green-backed goldfinches forage on 55 kinds of plant food, but the records show only 20 kinds of plant food eaten by the Lawrence. The contrast mainly is the result of differing abundance of the two species. The Lawrence goldfinch shows special preference for the seeds of fiddleneck, especially through the nesting season. In winter both species eat great amounts of chamise seeds. The nature of the food, and the manner of taking it, is conducive to taking large amounts of water. The habit of eating salt and sand is also related to alimentation in goldfinches.

These sociable goldfinches exhibit varied relationships with other kinds of birds. Observed examples of association with other species of birds on the Reservation were recorded frequently. For the green-backed goldfinch 29 species and for the Lawrence goldfinch 19 species provided clear examples of association that represented awareness of near approach or some more important response that would influence the birds involved.

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Winter Food of the Short-eared Owl in Central New York

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A group of short-eared owls (*Asio flammeus*) has occupied a small suburban park near East Syracuse, New York, for a number of winters. Residents living at the edge of the park reported seeing as many as 32 at one time. The writer first learned of this group in March 1953 and at that time there were about 14 owls in the area. In 1954 still fewer owls were present; the number was estimated at seven.

The park is irregular in shape and covers about 10 acres. It was planted with a row of spruce trees around the margin and small groups of spruce and cedars through the central part. These trees average about 20 feet in height and are crowded where they have not been thinned. The area is divided into two nearly equal parts by a highway. There are about a dozen homes adjacent to the park. The park and homes are completely surrounded with open fields that have been abandoned for agriculture for a number of years and are now covered with a heavy growth of grasses and weeds. There are a few scattered bushes in these fields and an occasional small tree.

On March 19, 1954, a large part of these fields had been burned over and a quick reconnaissance revealed many signs of mice. Runways were close together and many nests and nest sites were in evidence. Therefore well stocked hunting grounds were available within a short distance on all sides of the park.

Approximately 1000 pellets were collected from the roosting area in late winter of 1953 and 1954. When the first collection was made, in March 1953, only fresh or well-formed pellets were kept. During the period of this study the area was visited repeatedly and on no occasion was any other species of owl seen. The uniformity in shape, size, and structure of pellets also indicates only short-eared owls in the area. Interested residents were questioned and reported they had seen only one "kind" of owl.

METHODS

All pellets were brought into the laboratory where they were completely dried before being stored in tight tin cans for analysis at a later date.

Each pellet was weighed and measured.

To facilitate analysis each dry pellet was washed with hot water, which caused it to disintegrate quickly. Under agitation, the bones separated from the hair and the latter floated to the surface. Care was exercised to see that no bones or other definitive parts were lost. Bird bones are light and frequently float to the surface with the hair.

APPEARANCE AND COMPOSITION OF PELLETS

Pellets of the short-eared owl are very compact and fairly smooth-surfaced. In comparing the pellets of this species with those of other owls Kirkpatrick

and Conway state (1947) "The short-eared owl produces pellets with less recognizable contents than any other species due to extreme efficiency of digestion." They also mention the extreme compaction of the pellets making them comparatively smooth-surfaced.

All pellets appeared much alike even when their contents differed. Close inspection revealed that those containing bird remains were somewhat lighter in color and more powdery in texture. The feathers were unrecognizable except for an occasional quill tip. The breast bone, long bones and skull fragments were identifiable as well as the lining of the gizzard of starling remains. Hair withstood the digestive action quite well.

About 95 percent of the skulls were badly shattered; the brain case almost invariably broken. It seems likely that this reflects the manner in which prey is killed. Only a few pellets were complete with respect to skulls and correlated limb bones. In contrast Wallace (1948) found 70 percent of 254 barn owl pellets complete in this respect. This bears out Kirkpatrick and Conway (1947) who reported that a captive short-eared owl tore its prey into small bits before swallowing and therefore the pellets were irregular in content.

SHAPE AND SIZE OF PELLETS

Some of the variation shown in figure 1 no doubt is due to the peculiarities in pellet formation of the short-eared owl. They are in part diurnal feeders and cast frequent pellets. This is quite different from the pellet ejection of other species of owls. Banks (1884) and Etrington (1938) found that the great horned owl might eject pellets daily or only once in two or three days. Sensenig (1945) usually got a daily pellet from a barred owl. Various authors have reported two pellets per day for the barn owl. Chitty (1938) reports that the tawny owl in Europe ejects two pellets each night and none during the day. The irregular contents of the pellets in the short-eared owl add to their variation in size and form.

The pellets varied from half a gram to 10 grams and averaged 3.15 grams. The most constant measurement was the greatest diameter and this varied from 11 to 28 millimeters. The average diameter was 20.6 mm. The greatest

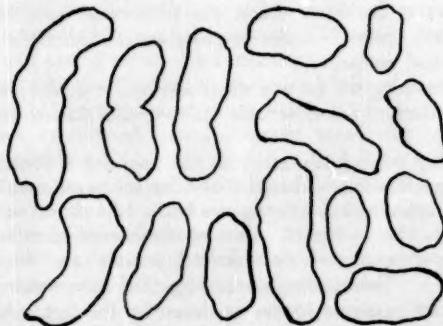


Fig. 1.—Variation in shape and size of pellets of the short-eared owl.

TABLE 1.—Animals represented in pellets

	Number	Percentage
Meadow mouse	1300	97.20
White-footed mouse	12	.89
Common shrew	3	.22
Short-tailed shrew	3	.22
House mouse	2	.15
Norway rat	1	.07
Birds	15	1.12
Crayfish	1	0.7
	1337	99.94

variation was in length. The minimum length was 18 mm, the maximum 81 mm and the average was 38.1 mm (fig. 1).

NUMBER OF ANIMALS REPRESENTED

In determining the number of animals represented the author used the number of skulls present. Kirkpatrick and Conway (1947) combined the contents of different pellets to make an animal. The more simple method was used in this study because of the large amount of fragmentation. Table 1 lists the findings.

The largest number of animals represented in a single pellet was six. This pellet contained 6 skulls, 9 jaws, 4 femurs, 7 innomates, and 6 humeri, of meadow mice (*Microtus pennsylvanicus*). The minimum represented in a pellet was a portion of one *Microtus*.

Certain factors are helpful in evaluating the findings listed in Table 1. Dice (1947) showed that the species of owls he worked with took more of the prey species easiest seen and that activity of the prey made it more vulnerable.

These factors help explain the relative numbers of each species taken. The low, level, open nature of the fields surrounding the roost may well account for so few individuals of other species of mice. One would expect a larger number of shrews to be taken unless the short-eared owls have a distinct preference for mice. Several studies of predators do indicate a preference for mice over moles and shrews.

The pellet containing the rat was small and only the two jaws and part of the skull were included, therefore only part of this animal may have been eaten.

There are many small birds active in the area for a considerable period after the owls begin hunting. The relatively few taken must indicate a preference for mice or difficulty in capturing the birds. As shown in table 1, most of the birds taken were sparrows. Five of these were identified as English sparrows by comparison with known skeletal material and five were smaller species of sparrows. Two starlings were identified in a similar manner and the other birds were passerine species as shown by the feet. All birds taken constitute only 1.2 percent of the prey species taken.

The piece of crayfish exoskeleton seems most unusual. There are small

ditches in the fields which contain water for considerable periods and crayfish may be present. None of the warm-blooded prey would contain so large a fragment and it therefore seems evident that the owl must have ingested it as a food item or possibly as an accidental inclusion with a warm-blooded prey item.

The bones gave information on age and sex as well as species. Many pellets were examined and discarded before these possibilities were realized. Sherman (1951) pointed out the sexual dimorphism in the pelvic girdle of *Microtus*. Applying his findings to this material the sex ratio in *Microtus*, as revealed by the pelvic girdles, was 405 males to 370 females. However, 284 were too badly broken to be identified as either sex and a few were questionable. It is quite likely that breakage is more severe in the female than

in the male since the female pelvic girdles are more fragile, as shown in fig. 2. The same figure also indicates some of the variability shown by each sex.

There were no distinct age groups indicated by the pelvic girdles and long bones but a fairly even gradation in size and maturity of these skeletal elements. The epiphysis from all but the older adults had separated by digestive action. The increase in size and thickness was more noticeable in the long bones than in the pelvic girdle. Fig. 2 shows these changes in the pelvic girdle. The age of the animals represented increases from left to right.

The long bones, skulls and pelvic girdles from 200 pellets were closely examined as to the age of the prey represented.

Twenty-seven of the 200 pellets contained the remains of adults only, 104 contained the remains of young mice only, and 69 pellets contained the bones of both adult and young mice. This means that young mice were present in 173, or 86.5 percent, of all pellets so studied. I believe this would reflect the age composition of the population fairly well. If we assume that the older mice were wiser in survival tactics it would mean that young mice made up over 86.5 percent.

The pellets examined were taken in February and March and since *Microtus* grow rapidly the presence of small animals at this time of year would indicate breeding into the middle of the winter. Hamilton (1937) says regarding this species of *Microtus* that at the height of the cycle with optimum densities prevailing, reproduction, although curtailed in winter, continues throughout the year.

No evidence of embryos was found in the pellets, however the efficient digestion of the owl would no doubt destroy such evidence.

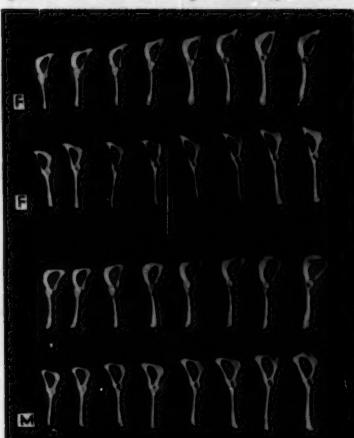


Fig. 2.—Sexual dimorphism and age differences shown in the pelvic girdle of *Microtus pennsylvanicus*.

CONCLUSIONS

The meadow mouse is the principal prey of short-eared owls during the winter in this particular area.

The amount of food consumed daily cannot be computed by the number of pellets formed.

A preference for mice over shrews is indicated.

Feathers are more completely digested than hair.

The number of birds taken as prey is very small even though the species is partly diurnal.

The winter food of the short-eared owl does not reflect the relative abundance of the various species inhabiting the hunting grounds.

Apparently most prey is killed by crushing the skull.

The short-eared owl is beneficial in its winter food habits in Central New York.

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Observations on the Mountain Chorus Frog, *Pseudacris brachyphona* (Cope) in Kentucky

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The mountain chorus frog, *Pseudacris brachyphona* (Cope) has been known to occur in Kentucky for many years, but the distribution of the species in the state has never been adequately defined. I have been collecting this species in the state as opportunity permitted for several years, particularly the past five years. During this time I have accumulated 363 specimens from the state; all are deposited in the zoological collection of the University of Kentucky.

This paper is a summary of field observations, data derived from the specimens, and literature records from the state.

Credit is due the Research Fund Committee of the University of Kentucky for financing several collecting trips, and many of my students, past and present, for assistance in collecting.

All measurements, except where otherwise noted, are expressed in millimeters, and are as defined by Smith and Smith (1952).

LITERATURE RECORDS

Dury and Williams (1933) listed two specimens from Madison County. Hibbard (1936), writing of Mammoth Cave National Park Proposed, encompassing parts of Warren, Barren, and Edmonson counties, stated that the species was ". . . common, especially around small streams and springs." Welter and Carr (1939) listed the species as "A very common spring frog" in northeastern Kentucky. Adams (1939) mentioned specimens from the Laurel-Clay County line, and the counties of Estill, Floyd, Greenup, Harlan, Knott, Johnson, Leslie, and Perry. Barbour and Walters (1941) stated "the chorus frog, *Pseudacris brachyphona* (Cope), is one of the most abundant spring frogs to be found in northeastern Kentucky." Barbour (1950) listed specimens from Elliott, Harlan, and Rowan counties, and stated ". . . common in the mountainous sections of eastern Kentucky." Barbour (1953) took 76 individuals from Big Black Mountain in Harlan County. Wright and Wright (1949) listed eastern Kentucky in the range of the species, and mentioned that the species seems ". . . to enjoy the carboniferous Pennsylvanian rocks . . . the Allegheny Plateau." Smith and Smith (*op. cit.*) implied that *P. brachyphona* occurs throughout eastern and central Kentucky.

DISTRIBUTION IN KENTUCKY

Pseudacris brachyphona occurs throughout the mountainous section of eastern Kentucky. In the northern half of this area, the western limit of the range is the well-defined western edge of the mountains (i.e., the western

TABLE 1.—Average measurements and ratios, by county, of 363
Pseudacris brachyphona from Kentucky

County	No. specimens	Snout-vent length	Tibia length	Head length	Head width	Tib. / SV	H. L. / SV	H. W. / SV
Bell	24	31.0	16.9	10.2	11.0	54.6	32.7	35.4
Breathitt	3	32.2	18.1	11.4	11.8	56.2	35.4	36.6
Carter	28	28.3	15.6	10.0	10.1	55.3	35.5	35.9
Casey	9	28.7	15.6	9.7	10.2	54.3	33.7	35.4
Edmonson	3	28.6	16.0	9.8	10.2	56.0	34.4	35.7
Elliot	5	27.5	14.3	9.2	9.6	51.9	33.4	34.7
Estill	3	28.5	15.7	10.3	9.7	55.2	36.1	34.1
Harlan	57	30.3	16.2	10.2	10.5	53.4	33.7	34.7
Laurel	3	29.7	16.3	9.9	9.6	54.8	31.1	32.3
Lee	23	29.4	15.7	9.7	9.8	53.4	32.9	33.2
Lewis	9	30.7	15.9	10.1	10.6	51.8	33.0	34.7
Lincoln	1	29.6	15.2	10.0	10.6	51.4	33.8	35.8
Madison	19	29.0	15.7	9.7	10.3	54.1	33.5	35.6
McCreary	9	29.7	15.9	9.8	10.3	53.4	32.9	34.5
Menifee	11	30.0	16.2	10.2	10.9	54.1	34.1	36.2
Nelson	1	26.5	15.0	9.8	9.7	56.6	37.0	36.6
Owsley	1	25.0	13.1	9.3	9.0	52.4	37.2	36.0
Powell	34	30.2	16.2	10.1	10.6	53.8	33.4	35.0
Pulaski	7	29.6	16.3	10.1	10.3	55.1	34.2	34.8
Rockcastle	59	29.6	15.8	9.8	10.2	53.2	33.2	34.3
Rowan	44	30.4	16.2	10.1	10.6	53.4	33.3	34.9
Whitley	3	28.8	16.3	10.3	10.5	56.8	35.8	36.4
Wolfe	7	28.5	15.2	10.0	9.8	53.4	35.2	34.4
State average ..		29.8	16.0	10.0	10.4	53.8	33.6	34.9

limit of the outcropping of the Pennsylvanian and Mississippian rocks in eastern Kentucky). Farther south, this limitation breaks down; the species extends westward roughly along the Green River valley at least to Morgantown in Edmonson county, and northward in the valley of Rolling Fork River at least into Nelson County. This western section of the range of *brachyphona* is almost exclusively Carboniferous and Devonian, but the species by no means extends throughout the outcropping of these rocks in the state (fig. 1).

CHARACTERS

Average size and ratios of the 363 specimens examined are: Snout-vent length, 29.8; tibia length, 16.0; head length, 10.0; head width, 10.4; tibia/snout-vent ratio, 53.8; head length/snout-vent, 33.6; head width/snout-vent, 34.9. Specimens were arranged by counties and averages of the above measurements and ratios determined (table 1).

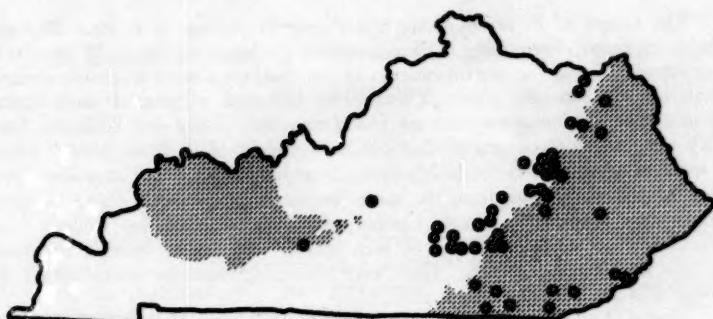


Fig. 1.—Distribution of *Pseudacris brachyphona* in Kentucky. Lined areas show the exposed Pennsylvanian rocks; circles the locality of specimens examined. Literature records are not included.

HABITAT

In Kentucky, *Pseudacris brachyphona* is essentially a creature of roadside puddles and ditches, but is frequently found in swampy areas, and occasionally along small woodland streams and about farm ponds. This frog is generally found only in wooded areas or along woodland edges; rarely is one found more than a few yards from a wooded area.

Elevation apparently has little bearing on the distribution of this species in Kentucky. However, the amount of tree cover apparently has a very definite bearing. In some areas, as along Rockcastle River in Laurel and Rockcastle counties, *P. brachyphona* is essentially confined to the valley. It is replaced in upland areas by *P. nigrita*. In this area, the uplands are more or less flat, cleared, and cultivated or pastured. The valleys are narrow, and well wooded. In other areas, as along Kentucky Highway number 92 in southern McCreary and Whitley counties, *P. brachyphona* is the species of the uplands, replaced in the valleys by *P. nigrita*. Here, the valleys are wide, and essentially cleared. The uplands are rugged, and generally well-wooded. In most of mountainous eastern Kentucky, the valleys are narrow, the hills steep, and well-wooded. Here, *P. nigrita* is absent, and in many areas one can travel for miles on a warm spring evening and rarely be out of hearing of the voice of *P. brachyphona*.

ASSOCIATES

Bufo terrestris americanus, *B. woodhousei fowleri*, *Acris gryllus crepitans*, *Hyla c. crucifer*, *H. v. versicolor*, *Pseudacris nigrita*, *Rana catesbeiana*, *R. clamitans*, *R. s. sylvatica*, *R. pipiens sphenocephala*, and *R. palustris* have been taken from breeding aggregations of *P. brachyphona*. *Hyla crucifer* is by far the most abundant species found in company with *P. brachyphona*. The only evidence of any direct relationships between *P. brachyphona* and any of its salientian associates was noted in Menifee County on March 21, 1953. A small *Rana catesbeiana*, collected from a breeding aggregation of *P. brachyphona* had devoured two of them.

The ranges of *P. brachyphona* and *P. nigrita* overlap in at least 20 Kentucky counties. Frequently both species may be heard calling from one area, but examination of the precise location of the choruses almost invariably reveals that they are separate, although sometimes less than a hundred yards apart. It is rarely that the two species are found together. Dury and Williams (*op. cit.*) took "forty specimens of *P. triseriata* and eight of *P. brachyphona*" from a roadside pond near Berea in Madison County. On only four occasions have I taken the two species from the same breeding aggregation. Three of these occurrences were in Rockcastle County; the fourth in Whitley County. In this latter case, one individual of each species was calling from a hat-sized puddle in a roadside ditch. Both were collected; intensive search failed to reveal additional individuals nearby.

Martof and Humphries (1955) stated that "both forms (*nigrita* and *brachyphona*) may call from the same general area; however, a little farther up into the hills (less than a half mile away) only *brachyphona* has been collected, and a little farther down in the lowlands, only *n. feriarum*. The sharp line of separation in the occurrence of these two forms is very impressive." I am in complete accord with these observations.

There is apparently no record of hybridization between these two species. This is not surprising, because of the relatively small area where the ranges of the two species overlap. This, coupled with the fact that it is only rarely that a breeding aggregation contains both species, makes the possibility of hybridization remote. It is quite conceivable that hybridization may occur; this is a matter of continuing research.

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A Distributional Study of *Pseudacris nigrita* in Kentucky

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The swamp chorus frog, *Pseudacris nigrita* Le Conte, has long been known to occur in Kentucky. Due perhaps in part to the paucity of specimens from the state, the population has been considered *P. n. triseriata* by numerous authors, among them Garman (1894), Dury and Williams (1933), Burt (1933), Wright and Wright (1946), and Barbour (1950).

Wright and Wright (*op. cit.*) indicated that the species is absent from central Kentucky, and Smith and Smith (1952) concurred in this opinion.

Largely during the past five years, a series of 328 specimens of *P. nigrita* has been collected from Kentucky, and is deposited in the zoological collections of the University of Kentucky.

Locality data of these specimens, plus numerous voice records of the author leave no doubt that *Pseudacris nigrita* is abundant in Kentucky south and west of a line from about Louisville south and east around the Knobs into the mountains about Berea, thence southeast through Pineville. The species is absent from the Bluegrass area, and from the greater portion of the mountains of eastern Kentucky (fig. 1). A related species *P. brachyphona* Cope, occurs throughout the mountains of eastern Kentucky, and overlaps the range of *P. nigrita* in portions of south-central Kentucky. This species, *P. brachyphona*, will be treated in a subsequent paper.

Examination of the specimens in the collections of the University of Kentucky, and a series of 57 specimens borrowed from the University of Louis-

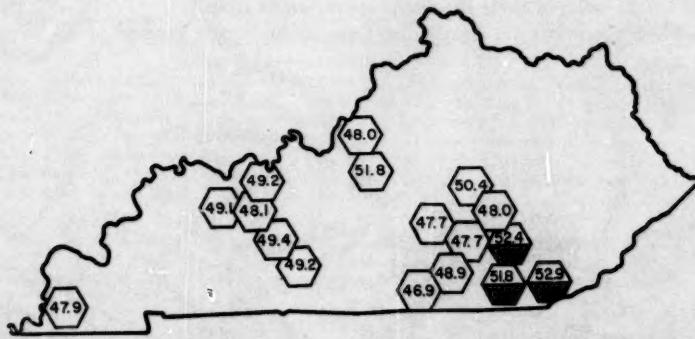


Fig. 1.—Average tibia/snout-vent ratios of *Pseudacris nigrita* from Kentucky. The location of the symbol indicates the geographic location of the county where the specimens were taken. Half-filled symbols represent *P. n. feriarum*; hollow symbols *P. n. feriarum* X *P. n. triseriata*.

ville, revealed that they do not fit the characters of *P. n. triseriata*, but rather key out to *P. n. feriarum* in Wright and Wright's (1949) key. However, the vast majority of the specimens do not precisely fit the characteristics of *P. n. feriarum* as recently redefined by Smith and Smith (1952).

The snout-vent length, the length of the tibia, the head length, and the head width of each specimen was determined, as defined by Smith and Smith (*op. cit.*). Average tibia/snout-vent length, head length/snout-vent length, and head width/snout-vent length ratios were then calculated for all specimens from a given locality. In no case was there an appreciable difference in average ratios from different localities within a single county; hence, the ratios from different localities within a single county were averaged to give a county-wide average. Individual ratios were calculated for 131 specimens from Jefferson and Pulaski counties. No appreciable difference was present.

The specimens from each locality were divided into three groups, striped, mottled, and plain, on the basis of pattern. Specimens exhibiting obvious stripes, whether broken or continuous, were considered striped; specimens whose dorsal pattern was spotted, but not obviously striped, were considered mottled; those specimens without a dorsal pattern were considered plain. The percentage of individuals in each group of the total number of specimens from the county was then calculated. Coloration fades rapidly in preservatives, but pattern much less so. The percentages derived from specimens taken in 1942 did not differ appreciably from those derived from specimens from the same county taken in 1953.

PSEUDACRIS NIGRITA FERIARUM (Baird)

Smith and Smith (1952) considered their Bell County specimens *P. n. feriarum*. Twelve specimens examined in this study from the adjoining counties of Bell, Laurel, and Whitley are all considered *P. n. feriarum* (fig. 2).

Tibia/snout-vent length, head length/snout-vent, and head width/snout-vent length ratios of these specimens are shown in table 1.

These specimens are among the most conspicuously marked of all exam-

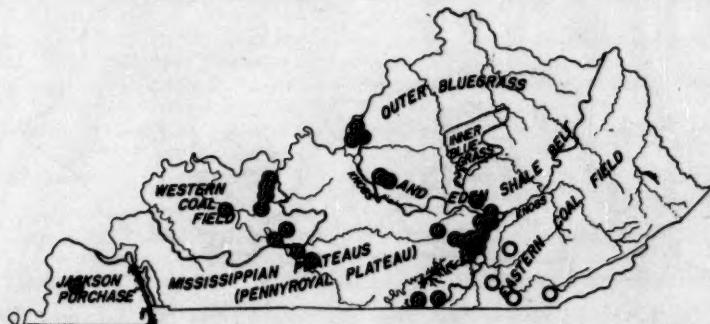


Fig. 2.—Locality records of *Pseudacris nigrita* in Kentucky. Hollow symbols represent *P. n. feriarum*, solid symbols *P. n. feriarum* X *P. n. triseriata*.

ined. Nine of them were obviously striped, and the remaining three were mottled.

Specimens examined.—Twelve Kentucky specimens were examined. BELL Co.: Six miles south Pineville, 4. LAUREL Co.: London, 4. WHITLEY Co.: Five miles west Williamsburg, 1; Cumberland Falls, 3.

PSEUDACRIS NIGRITA FERIARUM X TRISERIATA

Three hundred seventy-three specimens were examined that are considered intergrades between *P. n. feriarum* and *P. n. triseriata*. Body ratios of these specimens are shown in table 1. The distribution of the specimens and the average tibia/snout-vent length ratio of all specimens from each county are shown in fig. 1.

Smith and Smith (1952) considered specimens from Carlisle and Trigg counties to be *P. n. feriarum*. The 31 specimens examined from nearby Hickman County are certainly distinct from *feriarum* from eastern Kentucky, and except for a higher percentage of weakly striped individuals, are essentially inseparable from a large series of intergrades from central Kentucky.

Seven specimens from Garrard and Nelson counties are near *feriarum* in body ratios, but inasmuch as there are but few specimens available, and they are separated from *feriarum* in the state by an area where the population is composed distinctly of intergrades, they too are considered an intergrading population.

As one progresses westward across Kentucky, there is a fairly gradual and quite well marked decrease in percentage of striped individuals and a corresponding increase in percentage of plain individuals. The percentage of mottled specimens is variable, but shows no apparent correlation with locality. Specimens from Hickman County, in extreme western Kentucky, do not fit into the overall pattern, because of a high percentage of striped (albeit weakly so) individuals. These data are presented in table 2, where the counties are arranged in an east-west direction.

Specimens examined.—Three hundred and seventy-three Kentucky specimens were examined. BUTLER Co.: Five miles northwest Morgantown, 3; six miles south Tilford, 10. CASEY Co.: Two miles south Yosemite, 27. CLINTON Co.: Static, 2. GARRARD Co.: Five miles south Paint Lick, 2. HANCOCK Co.: Three miles north Lyonia, 50. HICKMAN Co.: Two miles south Beulah, 31. JEFFERSON Co.: St. Dennis, 6; Buechel, 6; Louisville, 57. MCLEAN Co.: Three miles north Livermore, 4. NELSON Co.: Six miles east White City, 2; four miles west Raywick, 1; two miles west Raywick, 2. OHIO Co.: Two miles north Hartford, 24; three miles south Dundee, 31; two miles north Dundee, 12. PULASKI Co.: Five miles east Eubank, 7; four miles east Eubank, 4; two miles east Eubank, 5; Eubank, 12; Science Hill, 9; two miles west Bandy, 24;

TABLE 1.—Body ratios of *Pseudacris nigrita* from Kentucky.
Extremes are shown in parentheses.

Area	No. specimens	T/SV	HL/SV	HW/SV
Bell, Laurel, and Whitley counties	12	52.4 (51.8-52.9)	34.2 (32.4-36.0)	34.0 (32.7-34.7)
Remainder of Kentucky	373	48.3 (47.7-51.8)	32.4 (31.1-34.8)	33.7 (31.8-36.5)

TABLE 2.—Percentages of striped, mottled, and plain *P. n. feriarum* X *triseriata* from 14 Kentucky counties. The counties are arranged in order from east to west.

County	Percentage of total sample			Number specimens
	Striped	Mottled	Plain	
Rockcastle	59	41	0	17
Pulaski	54	28	18	62
Garrard	50	50	0	2
Wayne	44	44	12	9
Casey	33	63	4	27
Clinton	0	100	0	2
Nelson	40	60	0	5
Jefferson	33	55	12	69
Warren	33	47	20	15
Butler	30	54	16	13
Ohio	18	30	52	67
Hancock	8	34	58	50
McLean	25	25	50	4
Hickman	48	48	4	31

Somerset, 1. ROCKCASTLE CO.: Three miles north Conway, 5; six miles north Mt. Vernon, 1; one mile south Brodhead, 1; two miles south Brodhead, 2; Quail, 8. WARREN CO.: Four miles north Hadley, 13; Floyd's Station, 2. WAYNE CO.: Four miles east Static, 9.

SUMMARY

Three hundred eighty-five specimens of *Pseudacris nigrita* from Kentucky were examined. Specimens from the southeastern counties of Bell, Laurel, and Whitley are considered *P. n. feriarum*. Elsewhere in the state, the population represents an intergradation between *P. n. feriarum* and *P. n. triseriata*. The species is absent from the Bluegrass area and the greater portion of the mountainous area of eastern Kentucky.

Acknowledgments.—I am indebted to many of my students, past and present, for assistance in the collection of the specimens. Mr. Rodney M. Hays, of Transylvania College, measured about a third of the specimens. Dr. William Clay of the University of Louisville made available a series of 57 specimens from Louisville. Credit is due the Research Fund Committee of the University of Kentucky for financial aid on collecting trips.

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Revision of the Genus *Stenamma* Westwood in America North of Mexico (Hymenoptera, Formicidae)

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Stenamma is one of the most primitive and also one of the smallest genera of myrmicine ants. The total number of described forms for the world is less than 30. This revision treats of 11 species for America north of Mexico, three of which are described as new. Although the genus was formerly thought to occur only in the Holarctic region, recently several forms have been described from the Neotropical region. However, some of these may eventually prove to be *Stenamma* in a broad sense only. The small number of recorded forms may be due to the small, well-concealed nests and the secretive habits of the ants. Headley (1952), for instance, in studying the ants of a locust grove in Ohio found *brevicorne* to be the second most common species in the number of colonies present, but he was able to locate colonies only by spreading bread crumbs on the surface of the soil and watching the foraging workers return to their nest with the food. Mary Talbot, in her unpublished studies of ants in the Drost Woods, St. Charles County, Missouri, in 1948-53, found three species of *Stenamma* in that area. Two of them, *schmittii* and *impar*, were common in the soil stratum. W. L. Brown has stated that, although he could find stray workers of one or more species in the spring or early summer in eastern Massachusetts, he had difficulty in locating colonies. Although *schmittii* is known to occur in the Edwin S. George Reserve in Michigan, Mary Talbot writes that she has not only been unable to find colonies but failed even to collect the species. The restricted habitats and drabness of color of the workers may also be responsible for the infrequent collecting of *Stenamma*. There appears to be no reason, though, why *Stenamma* should not be found in every one of our States, although records are still lacking from a number of them, especially the more central and southern States. Since the ants are confined largely to wooded areas, one should not expect to find them in all types of ecological habitats. In approximately the northeastern fourth of the United States four of our most common species are *brevicorne*, *schmittii*, *diecki*, and *impar*. Present records indicate that in our Western States *diecki* and *occidentale* are not uncommon.

Stenamma is represented by a fossil species, *berendti* Mayr of the Baltic Amber. Geologists assign the Baltic Amber to the Tertiary period, which is supposed to have existed about 60 million years ago. This single fossil species is known from two males only, which, peculiarly enough, have the same type of wing venation as our common North American *brevicorne* (Mayr) and not that of the common European *westwoodii* Westw. Ants of

the Baltic Amber had essentially the same general habits as our present-day forms; that is, they lived in colonies, some were of terrestrial habits, others arboreal, some forms attended plant lice, others did not. The lack of *Stenamma* workers in the Baltic Amber can be explained by the fact that the ants are noted for their terrestrial habits.

BIOLOGY

The general habits of our *Stenamma* are more or less stereotyped. The ants are usually confined to wooded areas, where their small and well-concealed nests may be found in objects lying on the surface of the soil such as logs, stumps, branches of trees or other woody debris, nuts and acorns. More commonly the ants nest in the soil beneath rocks, logs, moss, debris or humus. Their nests consist usually of only one to a few chambers (seldom more than an inch in width or length) placed in the upper 12-18 inches of the soil. The colonies are smaller than those of most other ants, ranging from a few dozen to several hundred adults, depending on the age of the colony and the time of year. The colonies are probably largest in midsummer to early fall. The largest colony that has come to my attention had 376 adults, including workers, males, and alate females.

Our knowledge of the life history and seasonal activities of *Stenamma* is based on random observations. During the winter a young colony may be expected to contain a mother queen, workers, and larvae. A few eggs have been found as late as October, but it appears doubtful that many, if any, of them overwinter. Although apparently accustomed to cool temperatures, the ants hibernate during the coldest months. In the spring, usually about April, activity begins again in the colony. The workers forage for food and the queen resumes egg laying. The overwintering larvae resume development and reach the adult stage by late spring or early summer. Adults from overwintering larvae appear a few weeks earlier than do those that develop from eggs laid in the spring. Apparently no males or alate females are produced in the younger colonies. In the older colonies these castes usually reach maturity between midsummer and early fall. There is reason to believe that males and alate females may take their nuptial flights as late as the middle of October. However, it is quite common for at least some of the males and alate females to overwinter in the parental colony and to take nuptial flight the following spring or later. It appears that some colonies produce only males, others only females, and still others a mixture of both males and females. As with many ants, it is not uncommon for males and alate females to fly at night and be attracted to artificial lights. It is believed that a single mated female is capable of establishing her colony alone and raising her first brood to maturity.

These ants feed on animal flesh, probably mostly arthropods. Brown and Wilson (unpublished observations) found the larvae of *diecki* feeding on a small dipterous larva determined by W. W. Wirth as probably an empidid, and also on what they thought might be a springtail. Cole and Wilson fed caged *diecki* workers collembolans and thysanurans. Donisthorpe (1927) kept a colony of *westwoodii* Westw. under observation in a cage for

at least five years and fed the ants flies and other insects, bread, cake crumbs, and honey. He found that they did not care much for honey but ate the other food readily. No reports have come to my attention that workers of *Stenamma* attend honeydew excreting insects or show any interest in feeding on honeydew. Donisthorpe found *westwoodii* docile and easy to rear and study in cages. It is my belief that our North American species would also be easy to study in cages. Since these ants have often been found within or in close proximity to the nests of other species, it has sometimes been assumed that they are associated with other ants, but this seems very doubtful.

Some new and interesting observations on *Stenamma schmittii* have been made by W. L. Brown at Lexington, Massachusetts. On October 10, 1954, he noted two foraging workers in leaf litter, and very near them two males though he was unable to locate their nest. One worker was carrying what appeared to be a small dipterous pupa, dead but in good condition; the other worker carried an immature but dead collembolan, *Tomocerus* sp., also in good condition. After studying the two workers in confinement, Brown remarked:

"The workers appear to have no set way of approaching the collembolans, but merely rush their prospective prey with mandibles opened wide. The collembolans usually manage to escape if attacked in an open space between the leaves in my jar, but if caught in a crevice or pocket, they have little chance of getting away. The attack by the ants is clumsy and hurried, in contrast to the finesse displayed by the collembola catching daekeiten, and there seems little doubt that springtails form only a part of their diet. . . . Use of the sting has not yet been observed but the rapid immobilization of the collembolan renders stinging a possibility to be considered when conditions of observations can be made more favorable than they were in the cases studied."

Upon returning to the exact spot where he made his first observations on *schmittii*, Brown made further observations as follows:

"Yesterday, November 14 was rather chilly and windy, and as before the *Prenolepis* were foraging in abundance in the leaf litter, as was the single specimen sent you [*schmittii*—author]. I have checked my notes on old collections and I find that in Pennsylvania all of my *Stenamma* were taken either early in the spring (mostly March) or else in October to December. I think the evidence is becoming very clear that *Stenamma* has unusual seasonal foraging habits geared to cool weather and resembling closely those of *Prenolepis imparis*. It is interesting to note the sudden abundance of *Stenamma* nests easily found in the forest belt where the hardwoods and northern coniferous forests blend into one another, in places that are cool, dark and moist, where few or no other ants are present. In such places, the ants forage actively in the soil cover even on cool, rainy days. Similar conditions are indicated by what I have heard about *Stenamma* collections in the high Smokies and in the Douglas fir forest of the Pacific Northwest."

TAXONOMY

Creighton (1950) has presented an excellent account of the confused and deplorable state of the taxonomy of our North American *Stenamma*. As he pointed out, unsuccessful attempts to develop a satisfactory classification for this group of ants were made by such eminent myrmecologists as Emery, Forel, and Wheeler. All these workers appear to have misinterpreted the significance of wing venation as a character for the differentiation of species, and consequently treated related but distinct forms as variants of a single species. To my knowledge Creighton was the first to indicate that many, if not all, of our named North American *Stenamma* are distinct species. He

apparently arrived at this conclusion largely on the basis of their geographical distribution, since he states, for example, that *schmittii*, *impar*, and *impressum* often occur in the same stations, a condition which would not be likely if these forms were subspecies. My study of the taxonomy and geographic distribution of these ants fully supports Creighton's contention. I have therefore treated all forms, both old and new, as species.

METHODS

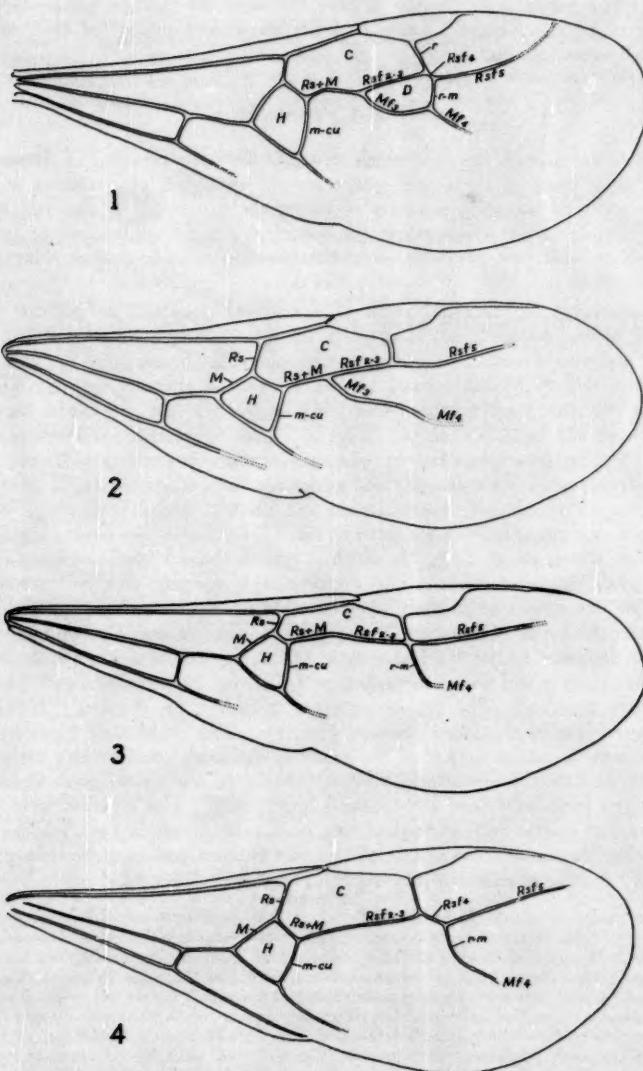
All specimens were studied with a Spencer stereoscopic binocular equipped with 9x ocular and 4.8x objective. The light was an alternating current transmitted through a G.E. automotive interior 6 cp. bulb. The position of the light and its intensity are very important. The sculpturing of the body of certain species, although highly characteristic, is best seen only from certain aspects and under certain light intensities. The longitudinal rugulae at the base of the gaster, for instance, are scarcely apparent when examined from one aspect but distinct from another. It is therefore best to examine body structures, sculpturing, pilosity, or color from a number of aspects.

Measurements are as follows: The length of the ant is the distance from the most anterior part of the head (the head being held in a normal position and not fully extended) to the most posterior part of the body; wings are not included. Head measurements exclusively do not include the mandibles. The length of the head is the distance through the central plane of the head from the most anterior border of the clypeus to a point touching an imaginary transverse line connecting the posterior border of each occipital lobe. The eye is not included in the greatest width of the head, this width being obtained by measuring transversely across the head on a line perpendicular to the axis of the head. The ommatidia counted in each eye are those lying only in the line of greatest diameter. Two thoracic lengths have been used, the greatest length from the anterior border of the pronotal collar either to the apices of the epinotal spines or to a point where the pedicel of the petiole joins the thorax. In the worker the greatest width of the thorax is represented by an imaginary transverse line connecting the two pronotal humeri. In the female and the male this measurement is taken just anterior to the first pair of wings. The narrowest width of the thorax occurs on the epinotum, where a similar transverse line connects the narrowest region of that part of the body.

TYPES STUDIED

Eleven species of *Stenamma* are included in this revisionary study, three of which are new. The new species are *huachucanum*, *meridionale*, and *occidentale*. I have been especially fortunate in being able to study worker types of all species except *impressum*. Two workers of this species from the U. S. National Museum collection were available for examination, but they are believed to belong to the original nest series, since not only do they very well fit Emery's description but they also bear the proper locality and determination labels, all in Theodore Pergande's handwriting. It should be noted, though, that the type locality of *impressum* is not Richs Springs, N. Y., as given by Emery (1895), but Richfield Springs (Otsego County), N. Y., as

PLATE 1



Figs. 1-4.—Anterior wing. 1. (Aberrant type), male of *S. brevicorne* (Mayr); 2. Female of *S. brevicorne*; 3. Male of *S. occidentale*, n. sp.; 4. Male of *S. westwoodii* Westw.

the labels on these two individuals show. In this revision *impressum* has been synonymized with *diecki*. I have not seen the dealate female type of *impar* or of *sequoiarum*. Table 1 shows the known castes for each of the eleven species.

WING VENATION

Since no attempt has been made to study the wing venation of *Stenamma* from other parts of the world except for the genotype, any remarks in this paper apply to the wing venation of the forms that occur in America north of Mexico. As the emphasis in the venational studies of ant wings is laid on the anterior pair of wings, only the venation of this pair of wings will be discussed.

Apparently the ancestral stock of *Stenamma* possessed an anterior wing similar to that on pl. 1, fig. 1, in which there was a single closed discoidal cell (H) and two closed cubital or submarginal cells (first cubital or first submarginal cell (C) and second cubital or second submarginal cell (D)). When vein r-m vanished from this wing, only Mf3 and possibly a trace of Mf4 were left as shown on pl. 1, fig. 2. This figure represents the normal type of wing now possessed by our species *brevicorne*, *impar*, *diecki*, and perhaps others (winged females and males are not yet known for *carolinense*, *forelocephalum*, *heathi*, *huachucanum*, *meridionale*, and *sequoiarum*). When vein r-m and possibly Mf4 are retained but Mf3 vanishes, we have a condition like that shown on pl. 1, fig. 3, which is typical for our species *schmittii* and *occidentale* (*neoarcticum*). The *occidentale* type may also be present in other of our species when their wing venation is known. There are thus two characteristic types of venation in the anterior wing of our *Stenamma*, which I shall designate as the *brevicorne* type (pl. 1, fig. 2) in which r-m is absent but Mf3 present and the *occidentale* type (pl. 1, fig. 3) in which r-m is present but Mf3 vanishes. The *brevicorne* type, according to Wheeler (1914), is similar to that of the fossil *berendti* (Mayr). The *occidentale* type, on the other hand, is similar to that of the common European species (also the genotype of *Stenamma*) *westwoodii* Westw. Owing to the instability of venation, wings are frequently seen with various aberrations. The anterior wing may possess two cubital cells instead of one or a wing in which the discoidal cell is lacking, or the second cubital cell and the discoidal cell may be only partly closed. Similar aberrations may occur in one or both wings.

Acknowledgments.—This revision is based on types or other material belonging to the following institutions and individuals: Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Museum of Comparative Zoology at Harvard College, United States National Museum, Naturhistorisches Museum (Vienna, Austria), Museo Civico di Storia Naturale (Genoa, Italy), Muséum d'Histoire Naturelle (Geneva, Switzerland), Cornell University, Canadian Department of Agriculture, Oregon State College, University of Nebraska, Iowa State College, Washington State College, Michigan State University, University of Kentucky, University of Georgia, Massachusetts State University, Illinois State Natural History Survey, North Carolina State Department of Agriculture, University of California Agricultural Experiment Station (Davis), Wm. F. Buren, L. F. Byars, A. C. Cole, W. S. Creighton, Robert E. Gregg, Mary Talbot, W. M. Mann, G. C. Wheeler, Mary Amstutz, A. E. Headley, Kurt Bohnsack, R. R. Dreisbach, P. B. Kannowski, Borys Malkin, Arnold Mallis, C. D. F. Miller, Arnold Van Pelt,

Vincent D. Roth, E. O. Wilson, Merle Wing, D. L. Wray, H. V. Weems, Jr., W. L. Brown.

The study would not have been possible had it not been for the full cooperation of these individuals and institutions. To them I wish to express my deepest gratitude. I am especially indebted to Mary Talbot for furnishing numerous individuals and valuable biological information, and to W. L. Brown for supplying important biological data and assistance in the interpretation of wing venation. The map and figures were prepared by Arthur D. Cushman.

STENAMMA Westwood

Stenamma Westwood, 1840, *Introduct. Mod. Class. Ins. Sup.* 2:83. Type: *Stenamma westwoodii* (Stephens, ms.) Westwood. Monob.

Asemorhoptrum Mayr, 1861, *Die Europäischen Formiciden*, p. 76. Type: (*Myrmica lippula* Nylander) = *Stenamma westwoodii* Westwood. Monob.

Theryella Santschi, 1921, *Soc. d'Hist. Nat. l'Afrique du Nord Bul.* 12:68. Type: (*Theryella myops* Santschi) = *Stenamma punctiventris* Emery. Monob.

Revisions: Emery, 1895, *Zool. Jahrb. Abt. f. System.* 8:297-301. Forel, 1901, *Soc. Ent. Belg. Ann.* 45:347-348. W. M. Wheeler, 1903, *Psyche* 10:164-168. Creighton, 1950, *Harvard Univ., Mus. Comp. Zool. Bul.* 104:133-138.

TABLE 1.—Known castes: The following castes have been described for the various species. Only dealate females are known for *meridionale* and *sequoiarum*.

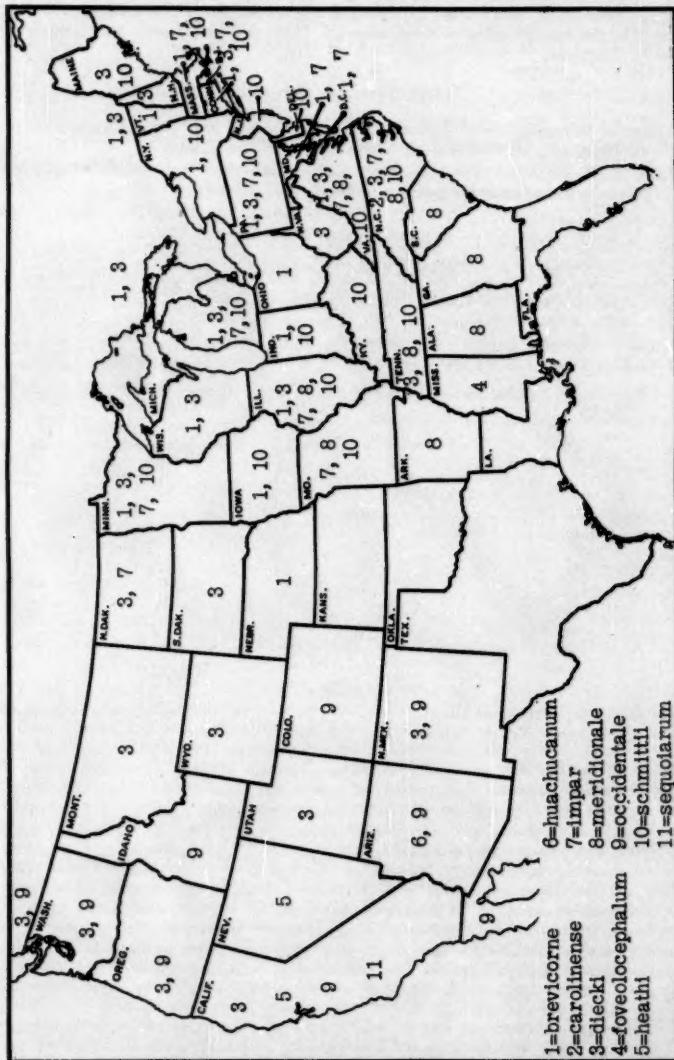
Species	Worker	Female	Male
<i>brevicornis</i> (Mayr)	x	x	x
<i>carolinense</i> M. R. Sm.	x	-	-
<i>diecki</i> Em.	x	x	x
<i>foveolocephalum</i> M. R. Sm.	x	-	-
<i>heathi</i> W. M. Whlr.	x	-	-
<i>huachucae</i> n. sp., M. R. Sm.	x	-	-
<i>impar</i> Forel	x	x	x
<i>meridionale</i> n. sp., M. R. Sm.	x	x	-
<i>occidentale</i> n. sp., M. R. Sm.	x	x	x
<i>schmittii</i> W. M. Whlr.	x	x	x
<i>sequoiarum</i> W. M. Whlr.	x	x	-

WORKER

Slender ants. Length 2.2-4 mm. Head usually subrectangular, 1.1-1.34 times as long as broad, with subparallel or moderately convex sides, rounded posterior corners and with an emarginate or almost straight posterior border. Antenna 12-segmented; apex of scape not attaining the posterior border of the head; funiculus noticeably enlarged toward the apex, the last four segments longer than the others but not forming a very distinct club; second through the 5th, 6th or 7th funicular segments broader than long. Mandible rather large, subtriangular, with 2-3 large apical teeth and usually 4-6 small, irregular basal teeth. Eye vestigial to moderately large, with from 3-12 ommatidia in its greatest diameter. Frontal carinae short, subparallel. Frontal area impressed, somewhat subtriangular, usually distinct. Clypeus with a pair of longitudinal carinae. Promesonotal suture indistinct or absent. Promesonotum usually rather strongly convex and prominent. Mesepinotal region with a distinct to a very pronounced impression. Epinotal spines varying greatly in shape and size, ranging from small and tuberculate to large and well developed. Petiole very distinctly pedunculate. Postpetiolar node larger than the petiolar node. Postpetiole separated from the gaster by a distinct constriction. Gaster, from above, sub-elliptical, without basal humeri. Body, exclusive of the gaster, usually with a rugulose or rugulose-reticulate sculpture and not smooth or strongly shining except in restricted areas. Hairs on the clypeus and front of the head usually longer than elsewhere on the body. Color ranging from light brown through reddish brown to blackish with the appendages and also the base and apex of the gaster commonly lighter.

FEMALE

Larger than the worker (3.2-4.6 mm in length) but otherwise similar in many respects. Differing especially in the larger eye, the greatest diameter of which is from 0.2-0.3 mm and contains 10-18 ommatidia, the possession of 3 ocelli on the vertex of the head and



Map 1.—Distribution of species of *Stenamma* in United States and contiguous countries

the usual thoracic modifications including the presence of wings. The anterior wing normally contains a closed cubital and discoidal cell but only an open radial cell. Occasionally the venation is aberrant; for a general discussion of this see section on WING VENATION. The normal venation of the anterior wing is of two types, the *occidentale* and the *brevicornis*. The *occidentale* type is characterized by the presence of the r-m cross vein but the absence of Mf3, the *brevicornis* type has the Mf3 but lacks the r-m cross vein. *S. schmitti* has the same venation as *occidentale*, and *diecki* and *impar* the same as *brevicornis*. The wing venation is not yet known for *carolinense*, *foveoloccephalum*, *heathi*, *huachucanum*, *meridionale* and *sequoiarum*.

MALE

Rather slender and small (approximately 2.5-3.5 mm in length). Head 1.1-1.5 times as long as broad, with rounded posterior corners and rounded posterior border; not flattened as in *Aphaenogaster*. Ocelli distinct but not large or prominently protruding above the general surface of the head. Eye placed anteriorly on the head, its greatest diameter approximately 0.2-0.3 mm. Antenna 13-segmented; scape approximately 0.2-0.37 mm in length and about as long as the combined lengths of the first 2.5-6 funicular segments; all funicular segments longer than broad, the funiculus enlarging toward the apex but the last 4 or 5 segments not forming a well defined club. Mandible bearing 2-5 teeth of variable size. Mayrian furrows usually present but sometimes feebly developed or obsolescent. Anterior wing with the same type of cells and veins as with the female of the same species, also subject to the same aberrations. Base of epinotum depressed or flattened in *brevicornis* and also tuberculate on each side; in the other species the base of the epinotum is straight, convex or concave and meets the declivity on each side to form a tubercle or else a rounded or angular protuberance. Legs long and slender, without noticeably enlarged femora and tibiae. Petiole distinctly pedunculate. Gaster without basal humeri. Genitalia not well developed or prominent, seldom exerted, cerci present. Pilosity light yellowish or grayish depending upon the intensity of the artificial light. Sculpture of body more feeble than that of the worker or female. Color of body ranging from brown through blackish brown to black, the appendages usually lighter.

KEY FOR THE IDENTIFICATION OF WORKERS

1. Dorsal surface of much of the first gastric segment with a peculiar shagreening and also scattered punctures which produce a subopaque effect; (epinotal spines rather long and especially acute; dorsal surface of thorax coarsely sculptured, usually of a rugulose-reticulate nature, with the interspaces often quite broad); Calif. and Nev.; pl. 3, figs. 9, 9a *heathi* W. M. Wheeler
1. Dorsal surface of the first gastric segment not as described 2
2. Base of the first gastric segment either without or with vestigial longitudinal rugulae (the length of the rugulae not exceeding 0.05 mm); (body brownish black to black, with lighter appendages, which give the ant a bicolored appearance; much of the body with the punctulate sculpture predominating; epinotum bearing extremely small or vestigial tuberculate spines; petiolar node, in profile, unusually high and very noticeably compressed anteroposteriorly); Ariz.; pl. 2, figs. 8, 8a *huachucanum* n. sp.
2. Base of first gastric segment with well developed or normal longitudinal rugulae 3
3. Large species (length 2.75-4 mm); eye usually with 5-12 ommatidia in its greatest diameter 4
3. Small species (length 2.3-3.5 mm); eye with 3-6 ommatidia in its greatest diameter 7
4. Rugulae or the rugulose-reticulate sculpturing of the promesonotum transverse in direction 5
4. Rugulae or the rugulose-reticulate sculpturing of the promesonotum usually longitudinal in direction 6
5. Eye large, 0.2 mm in its greatest diameter and with 10-12 ommatidia; base of epinotum subhorizontal; epinotal spines extremely short, blunt and tuberculate; N. C.; pl. 4, figs. 14, 14a *carolinense* M. R. Smith

5. Eye smaller, 0.15 mm in its greatest diameter and with 7-8 ommatidia; base of epinotum sloping; epinotal spines tuberculate but with rather acute apices; Miss.; pl. 4, figs. 16, 16a *forelocephalum* M. R. Smith
6. Petiolar node commonly subconical when viewed from above and behind; (base of epinotum often with a transverse welt; body usually subopaque); Nova Scotia to Va. and west to Nebr. and Minn.; pl. 4, figs. 13, 13a *brevicornis* (Mayr)
6. Petiolar node not usually subconical when viewed from above and behind, also rather compressed anteroposteriorly especially when viewed in profile (epinotal spines commonly unusually long and somewhat digitiform); Va. and S. C. west to Ill., Mo. and Ark.; pl. 4, figs. 15, 15a *meridionale*, n. sp.
7. Base of gaster with unusually long and rather well defined rugulae (some of which are 0.2 mm in length); postpetiole also with well defined longitudinal rugulae; (thorax coarsely sculptured, rugulose to rugulose-reticulate with the interspaces often as broad as 0.10 mm or more; body 3-3.5 mm in length and light brown to dark reddish brown in color); Calif.; pl. 3, figs. 11, 11a *sequoiarum* W. M. Wheeler
7. Base of gaster without unusually long or well defined longitudinal rugulae; if the postpetiole bears longitudinal rugulae these are not normally well defined 8
8. Thorax either shining in the promesonotum or the general surface of the thorax not dulled throughout by numerous, dense and distinct punctures 9
8. Thorax subopaque; the sculpturing highly variable but always of such a nature that the punctures are dense enough to dull the general surfaces regardless of their position or abundance 10
9. Small (2.3-2.7 mm in length); thoracic sculpturing weak; postpetiole seldom noticeably smooth and shining; (ommatidia of eye unusually coarse; petiolar node in profile subangular or angular); Mass. and N. C. west to N. Dak., Ill., and Mo.; pl. 2, figs. 6, 6a *impar* Forel
9. Larger (2.7-3.5 mm in length); thoracic sculpturing highly variable but seldom weak, the promesonotum usually distinctly shining; postpetiole usually smooth and rather strongly shining; Southeastern and Southwestern Canada and most of the United States except the Central and a few of the Southern States; pl. 3, figs. 10, 10a *deckeni* Emery
10. Sculpturing of the thorax other than the punctulations often very coarse; prothoracic humeri not well defined; postpetiole seldom entirely smooth or noticeably shining; N. Y. and Mass. to N. C., west to Minn. and Mo.; pl. 2, figs. 5, 5a *schmittii* W. M. Wheeler
10. Sculpturing of the thorax other than the punctulations usually weak; prothoracic humeri often well defined; postpetiole commonly smooth and shining; B. C. to Lower Calif. (Mex.), east to Idaho, Colo. and N. Mex.; pl. 2, figs. 7, 7a *occidentale*, n. sp.

STENAMMA SCHMITTII W. M. Wheeler

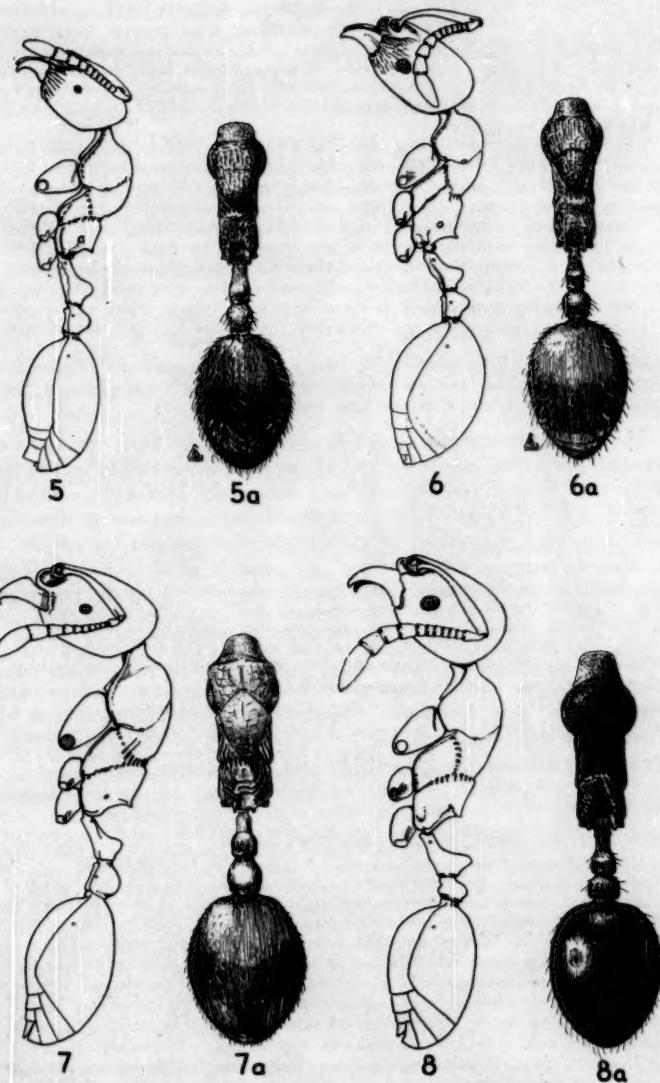
Stenamma brevicorne schmittii W. M. Wheeler, 1903, Psyche 10:167, worker. Weston and Wesson, 1940, Amer. Midl. Nat. 24:93. Gregg, 1944, Ent. Soc. Amer. Ann. 37:456, 464-465, worker. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, worker. M. R. Smith, 1951, In U. S. Dept. Agr., Monogr. 2, p. 795, worker.

Stenamma schmittii W. M. Wheeler, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:136, 138, worker.

WORKER (pl. 2, figs. 5, 5a)

Length 2.5-3.5 mm. Second through the sixth funicular segments broader than long, the last segment of the antennal club approximately as long as the combined lengths of the three preceding segments. Eye extremely small to very small, the greatest diameter 0.10 mm and composed of three to six ommatidia. Thorax, in profile, usually with a very pronounced mesoepinotal impression which is often 0.10 mm in length and proportionally

PLATE 2



Figs. 5-8.—Lateral view of worker with all segments of legs omitted except coxae and (a) dorsal view of worker with head and legs omitted. 5. *S. schmittii* Whlr.; 6. *S. impar* Forel; 7. *S. occidentale*, n. sp.; 8. *S. huachucanum*, n. sp.

as deep. Epinotum commonly sloping posteriorly, the base and declivity meeting to form a pair of distinct but variably sized spines, which range from about one-sixth to one-fourth the length of the base of the epinotum. Petiolar node, in profile, rounded to subangular resembling that of *impar* but perhaps not quite so extreme; from above and behind, although it resembles that of *impar*, it is usually blunter and more rounded. Postpetiolar node, from above, subcampanulate to subrectangular, with the bluntly rounded apex of the node directed somewhat posterodorsad. Longitudinal rugulae at the base of the gaster varying from obsolescent to moderately well developed, ranging in length from less than 0.10 mm to slightly more.

Frontal area smooth and shining. Front with posteriorly diverging, longitudinal striae, remainder of head largely reticulate or rugulose-reticulate, with punctate interspaces. Sides of thorax longitudinally rugulose and also densely punctate, the punctures sometimes predominating over the rugulae, especially in certain parts; mesopleuron often largely punctate. Thorax above, varying from fine to very coarsely rugulose-reticulate or rugulose with punctate interspaces; often the rugulae on the mesonotum have a longitudinal trend. Petiolar and post petiolar nodes largely densely punctate but not always opaque. The shagreening on the first gastric segment varies from obsolescent to moderately well developed, the sculpturing more evident in some lights than others. Head and thorax subopaque or opaque, the petiolar and postpetiolar nodes less so, the gaster smooth and shining.

Body highly variable in color ranging from a yellowish brown or light brown through reddish brown to almost blackish; appendages lighter, gaster usually light at the base and apex with an infuscated, transverse band midway of its length.

This is a highly variable species in many respects. Such variations especially apply to the size of the eye and the number of ommatidia in its greatest diameter; the number (usually 4-6) and size of the basal teeth of the mandibles; the size and shape of the mesoepinotal impression, size of the epinotal spines, shape and proportions of the petiolar and postpetiolar nodes. The color and sculpture of the body are very variable as is also the degree of development of the longitudinal rugulae and shagreening on the first segment of the gaster.

The worker can be distinguished by the size and structure of the eye; the nature and appearance of the sculpturing of the body; the usually well developed and very distinct mesoepinotal impression; shape and proportions of the petiolar and postpetiolar nodes. The worker is most apt to be confused with that of *impar*. It differs especially in the smaller eye, the larger and more coarsely sculptured and also more opaque body.

ALATE FEMALE

Similar to the worker except as described below.

Length 4.4-3 mm. Anterior ocellus located 0.35-0.40 mm back of frontal area. Antennal scape failing, by its greatest breadth or less, to attain the posterior border of the head. Greatest diameter of eye approximately 0.2 mm and with 12-14 ommatidia. Viewed frontally, the anterior border of the eye is located about 0.25-0.30 mm posterior to the base of the mandible. Thorax from the anterior border of the pronotal collar to the apices of the epinotal spines 1.45-1.55 mm in length, widest slightly anterior to the wing insertions where it measures 0.70-0.75 mm; humeri subangular. Venation of anterior wing similar to that of *occidentale*. Veins and stigma light brown or yellowish. Thorax with tuberculate to normal shaped spines which are 0.10 mm or less in length. Petiole, in profile, pedunculate with subangular to distinctly angular node. Postpetiole, in profile, 0.3 mm high, convex above, almost as high as long. Petiolar node, from behind, with dorsally converging sides and weakly rounded to subtruncate superior border. Postpetiole from 0.25-0.30 mm broad, approximately as broad as long.

Thorax above, coarsely rugulose-reticulate; the longitudinal rugulae somewhat convergent toward the middle of the anterior border of the mesonotum. Scutellum often more

finely sculptured than the mesonotum. Area above the epinotal spines transversely rugulose-punctulate. Side of the anterior coxa transversely rugulose-punctate. Petiolar and postpetiolar nodes above rugulose- or rugulose-reticulate, punctulate, subopaque. Much of the first gastric segment varying from finely reticulate and subopaque to smooth and shining (the reticulations more distinct in some lights than others). Frontal area and infraspinal area smooth and shining.

Pilosity yellowish to golden, fairly abundant, slender, consisting of variable lengthened hairs that are suberect to erect. Pubescence on legs and scapes rather dense.

Occasionally there may be infuscated spots on the head and thorax, or the head and thorax may be darker than the rest of the body. The gaster may vary from brown to blackish but the apex is apparently lighter than the remainder; commonly the darker portion gives the appearance of a broad, transverse band.

There is considerable variation in color as well as in some of the body proportions. As mentioned above much of the first gastric segment may be finely reticulate or else smooth and shining.

The female of this species is distinguished by its size, nature of the wing venation which is similar to that of *occidentale*, the peculiarly dull, subopaque appearance of the body and the subangular to angular node.

MALE

Length 3.3-3.5 mm. Head approximately twice as long posterior to the eyes as in front of the eyes. Eye large, convex, protuberant, 0.20-0.25 mm in length and more than 0.10 mm in width. Anterior ocellus located approximately 0.2 mm posterior to the frontal area. Clypeus convex above and bearing a longitudinal furrow or impression, the anterior border of the clypeus arched. Mandible subtriangular, with 3-4 distinct teeth. Scape exceptionally short, usually 0.23-0.25 mm long and approximately as long as the combined lengths of the first three funicular segments. Thorax from the anterior border of the pronotal collar to the articulation with the peduncle of the petiole, 1.2-1.5 mm in length; widest anterior to the articulations of the anterior wings where it measures 0.65-0.75 mm. Mesonotum with distinct Mayrian furrows, the parapsidal sutures indistinct to distinct but more commonly distinct. Epinotum, in profile, with concave basal surface, which is approximately 0.35-0.40 mm in length and meets the declivity in either an angle or an angular tubercle. Petiole, in profile, with the peduncle meeting the node above to form a bluntly rounded to distinct angle. Petiole and postpetiole, from above, slender in appearance but the postpetiolar node often almost as broad as long.

Frontal region of head to at least as far posteriorly as the anterior ocellus very finely longitudinally striated, remainder of the head, for the most part, densely and finely punctulate. Thorax largely punctulate; in some lights there are discernible above, on at least the posterior part of the mesonotum, very fine, longitudinal striae. Side of epinotum longitudinally to irregularly rugulose-punctulate. Petiolar and postpetiolar nodes above, largely smooth and shining; on the sides the punctures are more apparent but never dense. Dorsal surface of epinotum, petiolar and postpetiolar nodes, and gaster shining; remainder of body subopaque. Mesopleuron and anterior portion of mesonotum often shining, at least in some lights; the mesopleuron frequently smooth or very finely sculptured.

Pilosity consisting largely of short, suberect hairs; those on the anterior border of the clypeus unusually long.

Body blackish to black, with yellowish mandibles, antennae and tarsi; apex of the coxae and gaster, trochanters, and the articulations of the femora and tibiae lighter than the remainder of the segments.

Males vary considerably in size, proportions of the body, and sculpture. The scutellum is sometimes almost smooth and shining. The first segment of the gaster may bear fine reticulations or punctulations.

The male can be distinguished by the nature of the wing venation, which

is similar to that of *occidentale*, shape of the epinotum, which in profile has a concave basal surface that meets the declivity to form a pronounced angle or tubercle, the color of the body and appendages, and the nature of the sculpturing, especially that of the thorax.

Type locality.—St. Vincent, Pennsylvania (1½ miles SW of Latrobe in Westmoreland County). Described from workers collected by P. J. Schmitt.

Location of types.—American Museum of Natural History, Museum of Comparative Zoology at Harvard College.

Distribution.—This species has been recorded from Maine to North Carolina, west to Minnesota and Missouri.

Specimens studied: Two cotype workers; also 445 workers, 14 dealate females, 54 alate females and 33 males from localities other than the type locality.

BIOLOGY

Our knowledge of *schmittii* is based on fewer data than that of *brevicorne*. It appears, however, that it is primarily a woodland loving form which is capable of living in fairly dry to moist habitats. Colonies are usually found nesting in the soil beneath stones, logs, rotten wood, moss, leaf mould, and other debris and are often difficult to find. The species has been collected at altitudes ranging from only a few hundred feet to approximately 5,000 feet. Mary Talbot has excavated a number of colonies in the Droste Woods in St. Charles County, Missouri. She has found colonies apparently containing from only one to four chambers and at depths of 5 to 15 inches. It appears that there is only a single mother queen per colony. The largest colony examined, on September 29, 1950, consisted of four chambers at depths of 5, 6, 7, and 10 inches. The colony contained 310 workers, 31 alate females and 35 males, 9 eggs, and 67 larvae. No pupae were seen, nor was the mother queen found. Miss Talbot did not think that this was a hibernating colony. Her general observations on *schmittii* indicate that alate females and males are produced in late summer, by some colonies at least, and that these castes overwinter in the parental nest until the following spring. The most common if not the only immature stage in which the ant overwinters is the larval.

For further information on seasonal habits and feeding activities of *schmittii* the reader is referred to observations by W. L. Brown, page 135.

Stenamma occidentale, n. sp.

Stenamma neoarcticum Mayr, 1886, Zool.-Bot. Gesell. Wien, Verh. 36:454, alate female, male (not worker). Mayr, 1887, Zool.-Bot. Gesell. Wien, Verh. 37:628 (footnote), alate female, male. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, alate female, male.

?*Stenamma (Stenamma) westwoodi nearcticum* Mayr, Emery, 1895, Zool. Jahrb. Abt. f. System. 8:299-300, worker, dealate female.

Stenamma (Stenamma) nearcticum Mayr, Forel, 1901, Soc. Ent. Belg. Ann. 45:347, alate female, male.

Stenamma nearcticum Mayr, W. M. Wheeler, 1903, Psyche 10:165-166, alate female, male. W. M. Wheeler, 1917, Amer. Acad. Arts and Sci. Proc. 52:519, alate female, male. W. M. Wheeler, 1926, Ants, Columbia Univ. Press, N. Y., p. 150. M. R. Smith, 1930, Ent. Soc. Amer. Ann. 23:564-565, alate female, male. Mallis, 1941, South. Calif. Acad. Sci. Bul. 40:66. Falconer Smith, 1941, Pan-Pacific Ent. 17:24. Creighton,

1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:135, 138, alate female, male. M. R. Smith, 1951, In U. S. Dept. Agr. Monogr. 2, p. 795, alate female, male.

The European myrmecologist Gustav Mayr in 1886 (see reference above) described *Stenamma neoarcticum* on the basis of two workers, one each from New Hampshire and Virginia, and two winged females and two males collected in California. The following year, on page 628 of his *Südamerikanischen Formiciden* (see reference above), he stated that he considered the workers from New Hampshire and Virginia identical with those of *brevicornis* (*brevicorne*) and that the species would then stand on the basis of the females and males. Most myrmecologists, including myself, in accepting the facts as stated directly above have been in error. We have either overlooked or misinterpreted a statement in Mayr's original description reading as follows: "Die Beschreibung des Arbeiters bezeichne ich als fur die Art typisch." in which Mayr designated the worker caste as the type of the species. Therefore, as Mayr said, *neoarcticum* is a synonym of *brevicorne*. I have examined Mayr's type from New Hampshire and agree that it is *brevicorne*. I have also examined two of Mayr's California specimens, a winged female and a male labeled "Calif. Oct. 31, '83." The collection of the U. S. National Museum contains a pair of similar specimens which I believe to be a part of the original series. These four males and females I consider the same as the new species which I am here describing as *occidentale*.

WORKER (pl. 2, figs. 7, 7a)

Length 3.4 mm. Funicular segments 2 through 6 broader than long; last funicular segment longer than the combined lengths of the two preceding segments. Eye small, oval, approximately 0.10 mm in its greatest diameter with six ommatidia. Thorax, from above, slender, 1.2 mm in length from the anterior border of the pronotal collar to the junction with the petiole, broadest through the humeral angles (0.45 mm) and narrowest through the epinotum (0.35 mm), with pronounced humeral angles; in profile, the mesoepinotal impression is moderately well developed, approximately 0.10 mm in length and 0.05 mm in depth, base of epinotum distinctly sloping to meet the declivity and form two small, tuberculate spines which are 0.05 mm in length or less. In profile, the petiolar node is subangular; the postpetiolar node larger than the petiolar node and more convex in its anterior half than its posterior half, from above, the postpetiole is stout, almost as broad as long. Gaster with the apex more acute than the base, the latter lacking humeral angles.

Sculpturing of head and thorax very weak, subopaque (in some lights, however, part of the thorax is slightly shining), the head apparently more subopaque than the thorax, the propleuron is sculptured and subopaque and the mesopleuron largely reticulate; epinotal declivity postpetiole and gaster smooth and shining, the dorsal surface of the petiole, especially the anterior face, somewhat shining in some lights.

Hairs light yellowish or grayish depending upon the light, moderately abundant, of variable length, largely depressed or suberect, those on the front of the head and anterior border of the clypeus unusually long. Pubescence of legs and scapes distinct but depressed.

Head, thorax, petiole and postpetiole dark brown, legs and gaster lighter, the latter with a rather broad, infuscated, transverse band near its mid length.

Paratype workers differ from the holotype mainly in the proportions of the head which ranges from 1.15-1.25 times as long as broad; the length of the thorax, 1.05-1.2 mm; greatest width of the thorax, 0.4-0.45 mm; narrowest width of thorax 0.3-0.35 mm; epinotal spines 0.03-0.05 mm in length; mesoepinotal impression 0.03-0.05 mm in depth and the postpetiole from almost as broad as long to apparently as broad as long; length of body 2.8-3.4 mm.

Workers other than paratypes show considerable variation in a number of

characters, these variations are: Head 1.12-1.25 times as long as broad; thoracic length 1-1.10 mm, greatest width 0.5 mm; narrowest breadth 0.25 mm; greatest diameter of the eye ranging from 0.05-0.10 mm; mesoepinotal impression varying in size and shape, roughly U- or V-shaped and 0.10 mm long and about half as deep; epinotal spines 0.025 to 0.05 mm in length; pedicel of the petiole noticeably shorter and the petiolar node less high in some individuals than others; pronotum less flattened and without such prominent humeral angles; color ranging from light to dark brown with the anterior portion of the head, antennae, legs and usually the base and apex of the gaster lighter. Although the head, thorax and petiole are usually subopaque and the postpetiole smooth and shining, the former regions may be slightly shining in some lights.

This species can be distinguished in the worker caste by the following characters: Small eye with four to six ommatidia in its greatest diameter; distinctly angular prothoracic humeri; sloping base of the epinotum which meets the declivity to form two small, tuberculate spines which are 0.05 mm or less in length; subangular petiolar node (in profile); postpetiole (from above) almost as broad as long; weak sculpturing of the head and thorax; postpetiole smooth and shining.

ALATE FEMALE

Similar to the worker except as described below.

Length 4.5 mm. Ocelli small, not very distinct, the anterior ocellus located about 0.4 mm posterior to the frontal area. Antennal scape failing by less than its greatest diameter to attain the posterior border of the head. First funicular segment approximately as long as the combined lengths of the three succeeding segments; last segment of the club approximately as long as the combined lengths of the three preceding segments. Eye oblong, its greatest diameter approximately 0.20 mm and with 12-13 ommatidia. Thorax 1.6 mm in length from the anterior border of the pronotal collar to the apices of the epinotal spines, widest (0.8 mm) anterior to the points of articulation of the wings. Anterior wing hyaline, with light brown or yellowish veins and stigma and bearing a closed cubital and discoidal cell but only an open radial cell. Vein r_m present but M_2 lacking. Epinotal spines, from above, scarcely half as long as the distance between their bases; in profile, short (less than 0.10 mm in length), tuberculate, with the apex of each directed latero-posteriorly but scarcely dorsad. Petiole, in profile, pedunculate, the anterior and posterior faces of the node meeting to form a very distinct angle. Postpetiolar node, in profile, convex above, concave beneath, scarcely higher than long. Petiolar node, from above and behind, with dorsally converging sides and subtruncate superior border. Postpetiole, from above, approximately 0.143 times longer than broad, with anteriorly converging sides in its anterior two-thirds and subparallel sides in the remainder. Gaster, from above, widest near its middle, the first segment occupying most of the gaster.

Mandibles striato-punctate, subopaque in some lights, shining in others. Clypeus, frontal area, area beneath epinotal spines, and much of each mesopleuron largely smooth and shining. Gaster entirely smooth and shining. Head with rather fine, longitudinal rugulae extending posteriorly from the frontal area, the rugulae becoming divergent posteriorly and even attaining the occiput; remainder of the dorsal surface of the head rugulose-reticulate with dull interspaces bearing umbilicate punctures. Cheeks largely longitudinally rugulose. Prothorax transversely rugulose anteriorly and longitudinally rugulose on the sides. Mesonotum and scutellum largely longitudinally rugulose, the interspaces shining, at least in some lights. Mesoepisternum and side of the epinotum longitudinally rugulose, the latter with finely punctulate interspaces. Base of epinotum transversely rugulose, with punctulate interspaces. Posterior surfaces of petiolar and postpetiolar nodes and side of postpetiolar node longitudinally rugulose. Dorsal surface of postpetiolar node rather smooth and shining. Longitudinal rugulae at the base of the gaster less than 0.10 mm in length.

Body rather uniformly dark reddish brown, with even lighter appendages. Eyes black. Mandibular teeth, region around the ocelli, epinotal spines and (certain regions of the thorax, when viewed in some lights) blackish. Mayr described the female as black-brown, mandibles and clypeus rust-red, antennae and legs more yellowish red, partly with a touch of brownish.

The above description of the female is based on one of the two individuals described by Mayr as *neoarcticum*. Females from other localities show the following variations: Head 1.12-1.16 times as long as broad, occasionally with weakly emarginate posterior border; mandibular dentition highly variable with three prominent apical teeth and the number of irregular basal teeth or denticulae ranging from four to six; anterior ocellus located from 0.35-0.40 mm behind the frontal area; thoracic length 1.3-1.6 mm, with greatest width 0.6-0.7 mm; petiolar node, from above and behind, with dorsally converging sides and subtruncate superior border to subparallel sides and rounded superior border; postpetiole usually slightly longer than broad, occasionally as broad as long; vein r_m in apposition with or slightly distad of vein r ; prothorax more transversely rugulose at the humeral angles; body length 3.17-4.5 mm; head and thorax often darker than the petiole, postpetiole and gaster; the anterior portion of the head, antennae, legs and apex of gaster light brown or yellowish brown.

MALE

Length 2.9-3.1 mm. Eye large, oval, approximately 0.2-0.25 mm in its greatest diameter. Ocelli placed approximately 0.10 mm posterior to an imaginary transverse line connecting the posterior borders of the eyes. Frontal area distinct, longer than broad. Scape short, approximately 0.2-0.25 mm long, as long as the combined lengths of the first 2.5-3.5 funicular segments. Thorax measured similar to that of the worker, 1.25-1.3 mm long, widest at the base of the anterior wings, where it measures 0.65-0.7 mm. Mayrian furrows present but not strongly developed. Parapsidal sutures also present but only clearly seen in some lights. In profile, base of the epinotum distinctly concave to almost straight, approximately twice as long as the epinotal declivity and meeting the declivity in a distinct angle. Petiolar node, in profile, distinctly angular. Postpetiole, from above, approximately as broad as long.

Mesopleuron, much of epinotum, especially the base and declivity, dorsal surfaces of petiolar and postpetiolar nodes, and gaster, smooth and shining; most of head and thorax rather delicately sculptured and subopaque, especially in some lights.

Pilosity moderately abundant, of variable length, largely inclined or suberect.

Body blackish to black, with lighter mandibles, antennae and legs. Wings pale, with light brown veins and stigma.

Males from other localities differ from the above described paratypes as follows: Body length 3-3.5 mm; head 1.2-1.3 times as long as broad; frontal area present but not always very distinct; antennal scape (exclusive of the pedicel) 0.2-0.3 mm in length and as long as the combined lengths of the first 2.5-4 funicular segments; mandibles with 2-3 teeth; thoracic length 1.15-1.4 mm; base of epinotum approximately 1.5-2 times as long as the declivity; Mayrian furrows present but varying from weak, scarcely distinct to rather well developed; postpetiole from approximately as broad as long to broader than long; anterior wing venation of some individuals highly aberrant, the discoidal cell lacking in one or both wings, and also the equivalent of an extra (second) cubital cell present in one or both wings.

Type locality.—Rustlers Park, Chiricahua Mountains, Arizona, 8,500 ft., 8- (25-26)-52, Borys Malkin, under stone. Described from a holotype and 53 paratype workers and

14 paratype males, all of which have been deposited in the U. S. National Museum under No. 62394.

Distribution.—This species has been recorded from British Columbia to Lower California (Mexico) and from the Pacific Coast States eastward to Idaho, Colorado, and New Mexico.

SPECIMENS STUDIED: In addition to types, 270 workers, 1 dealate female, 48 alate females, and 82 males from localities other than the type locality.

BIOLOGY

Our records show that males as well as male and female pupae are found in the nest at least as early as late August (25-27). Winged females and males have been captured in flight at Lake Louise near Steilacoom, Washington, on September 21. Other winged females and males have been collected as late as October (29-31), but the conditions under which they were taken are not known; therefore it cannot be definitely said whether these sexed forms were produced during the current year or the year preceding. The species has been collected at altitudes ranging from 700 feet to as high as 9,000 feet. All known colonies are from the soil beneath rocks.

STENAMMA IMPAR Forel

Stenamma (Stenamma) brevicorne race *impar* Forel, 1901, Soc. Ent. Belg. Ann. 45:347-348, worker, dealate female.

Stenamma brevicorne impar Forel, W. M. Wheeler, 1903, Psyche 10:166-167, worker. M. R. Smith, 1947, Amer. Mid. Nat. 37:555, worker. M. R. Smith, 1951, In U. S. Dept. Agr., Monogr. No. 2, p. 795.

Stenamma impar Forel, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:136-137, worker. Talbot, 1951, Ent. Soc. Amer. Ann. 44:307 (part), Misdent.

WORKER (pl. 2, figs. 6, 6a)

Length 2.3-2.7 mm. Funicular segments 2 through 7 broader than long; last segment of antennal club approximately as long as the combined lengths of the three preceding segments. Eye subelliptical, approximately 0.10 mm in its greatest diameter and with 5-6 ommatidia; all ommatidia distinct and coarse in appearance. Thorax, in profile, with distinct to frequently pronounced mesoepinotal impression, the impression sometimes as much as 0.10 mm long and about half as deep. Base of epinotum meeting the declivity to form a pair of short, but distinct, variable sized, tuberculate spines which are borne on the epinotum as pronounced angles. Petiolar node, in profile, very distinctly angular; viewed from above and behind, the node is slender (often with dorsally converging sides), compressed antero-posteriorly, with truncate or weakly rounded superior border. Postpetiolar node, from above, almost as long as broad and with a subrectangular to subglobular appearance; the anterior two-thirds of the dorsum convex and somewhat anteroposteriorly compressed. Base of gaster bearing weakly developed, longitudinal rugulae which are usually 0.10 mm or less in length.

Frontal region of head with fine, posteriorly diverging, longitudinal striae which are scarcely discernible in some lights. Mandible longitudinally rugulose, with scattered, coarse punctures. Cheeks largely composed of longitudinal rugulae. Most of head bearing fine, rugulose-reticulate sculpture in which the interspaces are punctulate. The sculpturing of the head not always clearly defined because of the nature of the color of the head and the fineness of the sculpture. Thorax above, with a fine sculpture which largely ranges from longitudinally rugulose to rugulose-reticulate, that on the promesonotum usually of a longitudinally rugulose nature. Petiolar and postpetiolar nodes largely finely punctulate except for their dorsal surfaces which are usually shining, especially in certain lights. Frontal area and gaster smooth and shining and also much of the propleuron.

Body usually light brown or yellowish brown, occasionally dark brown; gaster however usually with an infuscated, transverse band near the middle.

The worker may vary in size and color as noted above. The gaster occa-

sionally lacks the infuscated band. The mesoepinotal impression varies from distinct to very pronounced. The epinotal spines although always distinct and tuberculate range from small and fine to moderately large and coarse. The petiolar node, when viewed from above and behind, may have sides which are subparallel or dorsally converging and the superior border of the node may vary from subtruncate to weakly rounded. The postpetiolar node, from above, although subrectangular to subglobular in appearance varies to some extent in proportion but is apparently slightly wider than long. The sculpturing of the body seems to be most variable on the thorax, especially on the epinotum, where it is often irregular although more commonly reticulate or rugulose-reticulate.

The worker of *impar* can in general be distinguished by its small size, slender form, fineness of body sculpturing, and usually light brown or yellowish brown color. Other important characters are: The rather small, coarsely faceted eye which measures approximately 0.10 mm in its greatest diameter and contains 5-6 ommatidia; funicular segments 2 through 7 broader than long; distinct to very pronounced mesoepinotal impression; the distinct but short, tuberculate spines which are angularly borne on the epinotum; the very strikingly angular petiolar node (in profile); and the weakly developed longitudinal rugulae at the base of the gaster.

ALATE FEMALE

Similar to the worker except as described below.

Length 3.2-3.5 mm. Antennal scape lacking its greatest diameter or less of attaining the posterior border of the head. Ocelli small, pale, the anterior ocellus usually located about 0.3 mm posterior to the frontal area. Eye oblong, usually 0.2 mm in its greatest diameter and with 10-12 ommatidia. Thorax from 1.2-1.5 mm in length measured from the anterior border of the pronotal collar to the apices of the epinotal spines, widest just anterior to the wing articulations where it measures from 0.6-0.65 mm. From above, the humeri are subangular. Anterior wings subopaque, with light brown or yellowish veins and stigma; venation similar to that of *brevicornis*. Base of epinotum, in profile, meeting the declivity in a very broad angle. Epinotal spines highly variable in size and shape, usually ranging from 0.05-0.10 mm in length. Petiole, in profile, pedunculate with very distinctly angular node. Postpetiole, in profile, scarcely longer than high, convex above and highest near its midlength. Petiolar node, from above and behind, usually with dorsally converging sides and weakly rounded or subtruncate superior border.

Mesonotum highly variable in sculpturing, ranging from smooth and shining in appearance to fine longitudinal rugulae and punctate interspaces to subopaque with coarser sculpture. The longitudinal rugulae on the scutellum commonly coarser and more apparent than on the mesonotum. Posterior part of epinotum, above, between, and below the epinotal spines often smooth and shining, occasionally finely sculptured above the spines. Propleuron largely longitudinally rugulose as are also the sides of the epinotum, the latter however with more distinctly punctate interspaces. Mesopleuron, especially the mesoepisternum, often largely smooth and shining. Petiole and postpetiole punctulate or rugulose-punctulate except for the rather smooth and shining nodes.

Hairs moderately abundant, slender, light yellowish, reclinate or suberect for the most part.

Body light brown or yellowish brown to dark reddish brown, with lighter appendages, eyes black, mandibular teeth and often the scutellum and wing articulations dark. Gaster highly variable in color, the apex usually light and the remainder of the gaster light brown to almost blackish, occasionally the gaster bears a dark, transverse band.

As the above description indicates, the female is subject to considerable variation, especially in color and sculpture. The variation in sculpturing

is especially noticeable on the head, mesonotum and mesopleuron. The length and width of the thorax seems to be fairly constant in the small number of specimens studied. I have not seen any individuals in which the base of the epinotum and declivity form a single plane as Forel has described.

The female can be distinguished from that of other forms by its small size (3.2-3.5 mm); commonly light brown or yellowish brown color; funicular segments 2 through 7 as broad as, or broader than long; greatest diameter of the eye usually 0.2 mm and containing therein 10-12 ommatidia; often rather smooth and shining mesonotum and mesopleuron; angular petiolar node (in profile), and a wing venation similar to that of *brevicornis*.

MALE

Length 2.9 mm. Head narrower in front of the eyes than behind the eyes, 0.35 mm in width. Posterior border of the eye approximately 0.25 mm anterior to the posterior border of the head. Eye large, convex, protuberant; from in front, usually more than 0.2 mm in length and 0.10 mm in width. Anterior ocellus located approximately 0.4 mm back of the anterior border of the clypeus. Clypeus convex above, the carinae vestigial or absent, the anterior border arched. Mandible slender, the masticatory border usually with three or four teeth, the first and second apical being the most distinct. Antennal scape (exclusive of the pedicel) approximately 0.3 mm in length and equal to the combined lengths of the first three or four funicular segments. Thorax, from above, 0.9 mm in length from the anterior border of the pronotal collar to the apex of the scutellum and 0.65-0.7 mm in width just anterior to the articulations of the wings. Mesonotal outline forming a broad arch anteriorly. Mayrian furrows distinct. In profile, base of epinotum meeting the declivity in a rounded angle; epinotal spines lacking, represented only by scarcely perceptible angular ridges. Petiole, in profile, pedunculate, with angular node. Petiolar and postpetiolar nodes, from above, rather narrow. Petiolar node, from behind, with subparallel sides and transversely truncate superior border. Postpetiolar node, from above, approximately as broad as long and of a subrectangular appearance.

Most of head finely punctulate, scutellum very finely longitudinally rugulose, side of epinotum irregularly sculptured, with the punctulation apparently dominating. Mandibles, much of mesonotum and mesopleuron, dorsum of petiolar and postpetiolar nodes, and gaster, smooth and shining.

Pilosity moderately abundant, slender, largely suberect or reclinate.

Body sordid light brown with lighter appendages.

The most notable variations were the length of the body, which ranged from 2.6-2.9 mm; the scape length 2.66-3 mm; length of thorax 0.8-0.9 mm; and width anterior to the articulations of the wings from 0.6-0.7 mm; eye, from in front, usually more than 0.2 mm in length, occasionally less, and usually more than 0.10 mm in width, occasionally less; color of body ranging from a pale, sordid brown to a much darker, sordid brown; wings subopaque to hyaline. One individual had an unusually small discoidal cell in one wing and none in the other.

Type locality.—Described from workers collected by A. Forel and Theodore Pergande on the Virginia bank of the Potomac River near Washington, D. C., while sifting damp leaves; also from a dealate female unassociated with other castes collected by Forel in Franklin Park, Boston, Massachusetts. I hereby designate Virginia as the type locality and have selected as a lectotype, a cotype worker from the Museum d'Histoire Naturelle, Geneva, Switzerland.

Location of types.—Museum d'Histoire Naturelle, Geneva, Switzerland, American Museum of Natural History, U. S. National Museum.

Distribution.—Massachusetts to Georgia, west to North Dakota, Illinois, and Missouri.

SPECIMENS STUDIED: One cotype worker from each of the museums mentioned above; also 423 workers, 12 dealate females, 11 alate females and 6 males from localities other than the type locality. I have not seen the dealate female cotype.

BIOLOGY

In her population studies of soil-nesting ants in the Droste Woods, St. Charles County, Missouri, from September to March during the years 1948 to 1953, Miss Mary Talbot found *impar* to be the most common *Stenamma*, *schmittii* second, and *meridionale* third. It is surprising that no individuals of *brevicornis* were taken. She is positive that in many instances she did not collect entire colonies of *impar*. Colonies or portions of colonies were collected at depths from 4 to 16 inches. Usually only one chamber was found, occasionally there were two. The largest number of workers collected from a colony was 109, the least 5. Only one mother queen was found per colony in 4 colonies. It appears from these and other records that most if not all colonies have only a single mother queen. Miss Talbot found that it is common for the larvae to overwinter in the nest; however, a half dozen or less eggs were found in 2 colonies as late as the middle of October. At the time of collection colonies were taken from both dry and damp soils. In the Edwin S. George Reserve in Livingston County, Michigan, Miss Talbot collected winged females and males from a colony on August 13, 1949. In the same locality K. Bohnsack collected 33 workers, 3 alate females and 1 male from a colony on August 19, 1949. Although Miss Talbot commonly found the species nesting in the soil, one of our records may indicate that *impar* also nests in rotten or faulty wood. This species has been collected at altitudes up to 4760 feet.

Stenamma huachucanum, n. sp.

WORKER (pl. 2, figs. 8, 8a)

Length 2.2-2.5 mm. Second to sixth funicular segments broader than long, the last funicular segment lacking very little of being as long as the combined lengths of the three preceding segments. Eye subelliptical, small for a *Stenamma*, approximately 0.10 mm in its greatest diameter, and with five to seven ommatidia. Mesoepinotal impression, in profile, distinct but not long or deep (less than 0.10 mm in length). Base of epinotum, in profile, sloping posteriorly to meet the declivity and forming a pair of extremely small (almost vestigial), tuberculate spines, a weakly developed but yet distinct carina usually leading from the mesoepinotal impression to each spine. Thorax, from above, with an obsolescent promesomotal suture. Petiolar node, from above and behind, unusually high, much compressed anteroposteriorly. Postpetiolar node, from above, as broad as, or broader than long, usually slightly wider anteriorly than posteriorly. Gaster often with a faint indication of basal humeri. Base of gaster either destitute, or almost destitute of longitudinal rugulae, the rugulae when present, less than 0.05 mm in length.

Body remarkable for its highly characteristic, unusually fine type of sculpturing. Front with extremely fine, scarcely discernible, longitudinal striae. Cheeks with longitudinal rugulae. Ground surface of head covered with extremely fine, rather dense punctures over which there is borne the scarcely apparent rugulose-reticulate sculpturing. Thorax above, also covered with extra fine punctures and in addition scarcely discernible longitudinal rugulae. Base of epinotum with fine, transverse striae in addition to the very small punctures. Petiole and postpetiole largely covered with very small punctures. Frontal area, clypeus, mandibles, propleura and gaster shining. In some lights the legs are even shining and there are also small, scattered shining areas on the thorax, petiole and postpetiole.

Hairs of variable length, light yellowish or grayish, moderately abundant and suberect to erect.

Body brownish black to black with lighter antennae and legs, the two colors contrasting to such an extent as to give the worker a bi-colored appearance. Gaster brownish at the base and apex with a blackish, transverse band in the middle.

The worker of this species varies in the following characters: Proportions of the head; number of ommatidia in the greatest diameter of the eye; shape and number of teeth of the mandible; development of the mesoepinotal impression and the epinotal spines; color of the gaster, the base often being blackish instead of brown.

The species is distinguished by the following characters: Small eye for a *Stenamma*, the greatest diameter of which is approximately 0.10 mm and has 5-7 ommatidia; very weakly developed clypeal carinae and mesoepinotal impression; pair of extremely small (almost vestigial) tuberculate epinotal spines; the unusually high petiolar node which is much compressed anteroposteriorly; base of gaster almost destitute of longitudinal rugulae, these when present or well developed apparently never exceeding 0.05 mm in length; bicolored appearance, and the delicate sculpturing of the body.

Type locality.—Head of Carr Canyon, Huachuca Mts., Ariz., 8,000 ft., 7-24-50, W. S. Creighton. Described from a holotype and 14 paratype workers.

Location of types.—The holotype and eight paratype workers are in the collection of the U. S. National Museum under No. 62393. The remaining paratypes are in the collection of W. S. Creighton.

Distribution.—In addition to the type locality this new species has also been collected at Webber's Cabin, Mt. Lemon, S. Catalina Mts., Ariz., 7,500-8,500 ft., 7-27-17 by the Cornell University Expedition of 1917.

SPECIMENS STUDIED: In addition to types, five workers from the Cornell University collection referred to above.

STENAMMA HEATHI W. M. Wheeler

Stenamma brevicorne heathi W. M. Wheeler, 1915, Amer. Mus. Nat. Hist. Bul. 34:410, worker. W. M. Wheeler, 1917, Amer. Acad. Arts and Sci. Proc. 52:520. Mallis, 1941, South. Calif. Acad. Sci. Bul. 40:66. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, worker. M. R. Smith, 1951, In U. S. Dept. Agr. Monogr. No. 2, p. 795. Cook, 1953, Ants of California, Palo Alto, p. 103, worker.

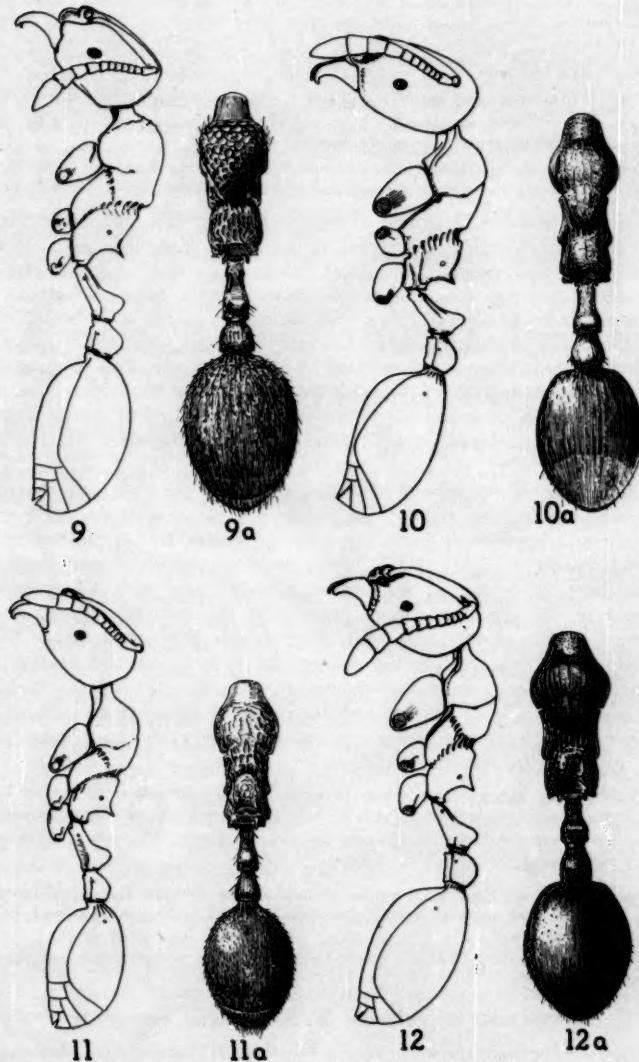
Stenamma heathi W. M. Wheeler, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:136-137, worker.

WORKER (pl. 3, figs. 9, 9a)

Length 2.5-3.3 mm. Second to 6th funicular segments broader than long, the last funicular segment almost as long as the combined lengths of the three preceding segments. Eye subelliptical, approximately 0.10 mm in its greatest diameter which contains from four to six ommatidia. Thorax, in profile, with variable sized mesoepinotal impression which is sometimes well pronounced and approximately twice as long as deep. Base of epinotum distinctly sloping posteriorly. Epinotal spines well developed, slender, with acute apices, approximately 0.25 to 0.33 the length of the base of the epinotum. Petiolar node, in profile, angular; from above and behind, varying from subrectangular to subconical, with truncate or weakly emarginate superior border. Postpetiolar node, from above and behind, as broad as long or broader than long, with subparallel sides except in the anterior third or fourth where the sides converge anteriorly.

Much of the head reticulate-punctate but the sculpturing not always easily seen because of the color of the head. Frontal striae present but also not always clearly discernible. Thorax above coarsely and rather irregularly reticulate, many of the interspaces often

PLATE 3



Figs. 9-12.—Lateral view of worker with all segments of legs omitted except the coxae and (a) dorsal view of worker with head and legs omitted. 9. *S. heathi* Whlr.; 10. *S. diecki* Emery; 11. *S. sequoiarum* Whlr.; 12. *S. impressum* Emery = (*diecki*).

quite broad; rugulae on the anterior portion of the prothorax quite often transverse and the rugulae on the promesonotum frequently with a longitudinal trend. Petiolar node rugulose-punctate to rugulose-reticulate, punctate; dorsal surface of postpetiolar node similarly sculptured. Longitudinal rugulae at the base of the gaster not as long and prominent as in *sequoiarum*. Much of the first gastric segment with a shagreening and scattered punctures which gives this region a subopaque effect, especially in certain lights. Frontal area, clypeal furrow, epinotal declivity and gaster, except at noted, smooth and shining.

Hairs light yellowish or grayish, moderately abundant, but not obscuring the ground surface of the body; apparently most abundant on the gaster.

Body and appendages varying from yellowish brown or light reddish brown to dark reddish brown; the gaster usually scarcely darker than the remainder of the body.

The most notable variations in the worker are: The proportions of the head; the number and shape of the teeth on the mandible; the number of ommatidia in the greatest diameter of the eye, this ranging from about 4-6; the mesoepinotal impression often pronounced, about twice as long as deep but occasionally smaller and less well defined; petiolar node when viewed from above and behind commonly subrectangular but occasionally subconical; post-petiolar node from about as broad as long to broader than long; sculpturing on the thorax highly variable as is also the color of the body. The single Nevada worker is dark reddish brown with a blackish, first gastric segment; this segment is also more opaque than ordinarily because of the nature of the sculpturing.

The worker of *heathi* can be distinguished by the following characters: It is commonly smaller (2.5-3.3 mm) than that of some of the other forms; the body and appendages including even the gaster are an almost uniform yellowish brown or light reddish brown to dark reddish brown; the eye is approximately 0.10 mm in its greatest diameter and with 4-6 ommatidia; the base of the epinotum slopes posteriorly; the epinotal spines are well developed, rather slender and with acute apices; the petiolar node is distinctively angular in profile; the postpetiolar node is usually as broad as, or broader than long; the coarse and rather irregular reticulate sculpturing of the thorax, especially of the promesonotum; the shagreening and coarse scattered punctures of the first gastric segment which gives this region a subopaque effect, especially in certain lights.

Type locality.—Kings River Canyon (Fresno County), California. Described by W. M. Wheeler from 25 workers taken from a single colony by Professor Harold Heath.

Location of types.—American Museum of Natural History, Museum of Comparative Zoology at Harvard College, U. S. National Museum.

Distribution.—California and Nevada. In addition to the type locality this species is known from the Yosemite and Sequoia National Parks of California and from Washoe County, Nevada.

SPECIMENS STUDIED: Nineteen cotype workers; also 36 workers from localities other than the type locality.

Stenamma sequoiarum W. M. Wheeler, new status

Stenamma brevicorne sequoiarum W. M. Wheeler, 1917, Amer. Acad. Arts and Sci. Proc. 52:520, worker, dealate female. Mallis, 1941, South. Calif. Acad. Sci. Bul. 40:66. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, worker. M. R. Smith, 1951, In U. S. Dept. Agr. Monogr. No. 2, p. 795.

Stenamma diecki sequoiarum W. M. Wheeler, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:136-137, worker, dealate female.

WORKER (pl. 3, figs. 11, 11a)

Length 3-3.5 mm. Eye rather small for a *Stenamma*, subelliptical, usually composed of four or five ommatidia in its greatest diameter, which is approximately 0.10 mm. Second to fifth funicular segments broader than long, the last funicular segment not as long as the combined lengths of the three preceding segments. Thorax, in profile, with distinct but variable sized mesoepinotal impression, the impression most often about twice as long as deep. Epinotum bearing two well developed spines which are approximately one-fourth to one-third the length of the base of the epinotum. Petiolar node from above and behind, usually somewhat subconical. Postpetiolar node, from above, subcampanulate, usually with the appearance of being longer than broad.

Sculpturing of head appearing rather weak and indistinct, probably due in part to the general color of the head, frontal striae fine but perceptible. Thorax, from above, very coarsely rugulose-reticulate, the sculpturing on the promesonotum often taking a longitudinal trend, the interspaces often very wide (sometimes as wide as 0.10 mm or more) and rather smooth and shining. Front coxa with distinct oblique or transverse rugulae. Postpetiole bearing sharply defined, longitudinal rugulae. Base of gaster with prominent, longitudinal rugulae, some of which are frequently as long as 0.2 mm or more. Rugulae on postpetiole and gaster sometimes not very distinct due to the color of these parts. Frontal area, clypeal furrow, epinotal declivity and gaster, smooth and shining. Rear of head, thorax, petiole and postpetiole weakly to rather strongly shining, according to the nature of the light.

Hairs on body moderately numerous but not obscuring the ground surface, apparently more abundant on the head and gaster than on the thorax. Appendages with distinct but rather closely appressed pubescence.

Head and thorax light brown or yellowish brown to reddish brown. Petiole, postpetiole and legs yellowish. Gaster brown or blackish, usually with an even darker, transverse, median band.

Variations are as follows: The head varies from 1.10 to 1.25 times as long as broad; the basal teeth of the mandible vary in size and number, usually being from four to six; the mesoepinotal impression is usually distinct and approximately twice as long as deep but occasionally may be smaller; sometimes there is a small transverse welt at the base of the epinotum following the mesoepinotal impression, color of the head and thorax ranges from a light brown or yellowish brown to a reddish brown.

The worker can be distinguished by the following characters: Eye rather small for a *Stenamma*, approximately 0.10 mm at its greatest width and with four or five ommatidia; epinotum with two well developed spines which are from one-fourth to one-third the length of the base of the epinotum; petiolar node slender and high, subconical; postpetiolar node subcampanulate, with the appearance of being longer than broad and bearing sharply defined, longitudinal rugulae; thorax above very coarsely rugulose-reticulate, the sculpturing on the promesonotum often taking a longitudinal trend, the interspaces variable in size but often 0.10 mm or more in width and rather smooth and shining; base of gaster with prominent, longitudinal rugulae, some of which are as long as 0.20 mm or more; head and thorax light brown or yellowish brown to reddish brown.

DEALATE FEMALE

Similar to the worker except as described below.

Length 4.3 mm. Eye slightly exceeding 0.2 mm at its greatest diameter and with 14 ommatidia. Thorax 1.65 mm in length from the anterior border of the pronotal

collar to the apices of the epinotal spines; widest slightly anterior to the wing insertions where it measures approximately 0.8 mm. Prothoracic humeri lacking. Epinotal spines, from above, stout, with blunt tips, the space between the tips about three times as long as the length of the spines. Petiolar node, from above and behind, not so slender or subconical as in the worker. Postpetiole subcampanulate, about as broad as long.

Propleuron with coarse, widely spaced oblique rugulae which have a posteroventral trend. Mesopleuron and side of epinotum with similar but longitudinal rugulae, those on the mesopleuron however not as coarse as on the side of the epinotum. The rugular interspaces are so finely sculptured that they are all rather shining. Pronotum and dorsal surface of epinotum coarsely and transversely rugulose, with the interspaces similar to those on the side of the thorax.

Color similar to worker except for darkened areas around the ocelli and wing insertions.

Wheeler gave the length of the dealate female which he described as 3.6 mm.

Type locality.—Muir Woods on Mt. Tamalpais (near San Francisco), California. Wheeler described the dealate female and numerous workers from several colonies that were found nesting under stones among the large redwood trees.

Location of types.—American Museum of Natural History, Museum of Comparative Zoology at Harvard College, U. S. National Museum and the personal collection of W. M. Mann.

Distribution.—Known from the types and from three individuals collected from the Sam P. Taylor State Park, Marin County, California on October 24, 1953 by Vincent D. Roth, these individuals having been obtained from redwood litter.

SPECIMENS STUDIED: Twenty-two cotype workers; also the two workers and one dealate female collected by Vincent D. Roth.

STENAMMA DIECKI Emery

Stenamma (Stenamma) westwoodi diecki Emery, 1895, Zool. Jahrb. Abt. f. System. 8:300, worker, dealate female.

Stenamma brevicorne diecki Emery, Forel, 1901, Soc. Ent. Belg. Ann. 45:347, worker, dealate female. W. M. Wheeler, 1903, Psyche 10:165-168, all castes. W. M. Wheeler, 1917, Amer. Acad. Arts and Sci. Proc. 52:519-520. Falconer Smith, 1941, Pan-Pacific Ent. 17:24. G. C. and E. W. Wheeler, 1944, N. Dak. Hist. Quart. 11:244. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, worker. M. R. Smith, 1951, *In U. S. Dept. Agr.*, Monogr. No. 2, p. 795.

Stenamma diecki Emery, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:133-136, worker, female. G. C. and J. Wheeler, 1953, Ent. Soc. Wash. Proc. 55:50-51, pl. 1, figs. 1-13, larva. Procter, 1938, Biol. Survey of the Mt. Desert Region, p. 433, male, Wistar Inst. Anat. and Biol., Philadelphia (misdet.).

Stenamma (Stenamma) westwoodi diecki impressum Emery, Emery, 1895, Zool. Jahrb. Abt. f. System. 8:301, worker. New Syn.

Stenamma (Stenamma) brevicorne diecki impressum Emery, Forel, 1901, Soc. Ent. Belg. Ann. 45:347.

Stenamma brevicorne diecki impressum Emery, W. M. Wheeler, 1903, Psyche 10:165, 167, worker. Dennis, 1938, Ent. Soc. Amer. Ann. 31:284, 304. Cole, 1940, Amer. Midl. Nat. 24:14, 15, 18, 19, 29, 48, worker. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, worker. Cole, 1950, Tenn. Acad. Sci. J. 25:297.

Stenamma brevicorne impressum Emery, Buren, 1944, Iowa State Col. J. Sci. 18:284, worker. Gregg, 1946, Amer. Midl. Nat. 35:749. M. R. Smith, 1951, *In U. S. Dept. Agr.* Monogr. No. 2, p. 795.

Stenamma impressum Emery, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:134, 138, worker.

WORKER (pl. 3, figs. 10, 10a)

Length 2.7-3 mm. Funicular segments 2-7 broader than long; last funicular segment approximately as long as the combined length of the two preceding segments. Eye rather small, oval, approximately 0.10 mm at its greatest diameter and with four or five ommatidia. Thorax 0.9-0.966 mm in length from the anterior border of the pronotal collar to the apices of the epinotal spines; broadest through the prothorax (0.40-0.45 mm), narrowest through the epinotum (0.3 mm). Thoracic humeri subangular. Epinotal spines, from above, small, with acute apices, the spines approximately 0.05 mm in length but shorter than their interbasal distance. Epinotal spines, in profile, distinct but not large, subtriangular, with their apices not especially directed dorsally. In profile, meso-epinotal impression distinct but not large, scarcely 0.10 mm in length and hardly half as deep. Base of epinotum sloping posteriorly. Petiolar node, from above and behind, with dorsally converging sides and weakly rounded or almost straight superior border. Postpetiole, from above, subcampanulate, approximately 0.25 mm in length and 0.20 mm in breadth. Petiole, in profile, with rather short pedicel and a subangular node. Postpetiole, in profile, varying from about as long as high to not noticeably longer than high. Gaster, 0.9 mm in length, with the first segment occupying most of the dorsal surface.

Sculpturing of head rather weakly defined, consisting of a number of small longitudinal rugulae in front which extend to the occiput or very near it, areas to the side of this more rugulose-reticulate with weakly punctulate interspaces, which are subopaque to opaque; below and median to the eye the longitudinal rugulae are very coarse. Mandible longitudinally rugulose and also with scattered punctures which in some lights appear rather coarse. Promesonotum with rather well defined, distinct and rather widely spaced longitudinal rugulae, the interspaces so feebly sculptured as to appear shining or only weakly opaque, this depending largely upon the nature of the light; some of them form a transverse arch on the anterior border of the pronotum, especially on the pronotal collar and also dorsad of the collar. Pronotal collar largely punctulate. Base of epinotum more irregularly sculptured. Sides of the thorax, especially the meso- and metapleuron, longitudinally rugulose, the punctulate interspaces somewhat coarser on the mesopleuron. Propleuron more weakly sculptured and in some lights rather shining. Most of the dorsal surface of the postpetiolar node rather smooth and shining, the sides and extreme posterior border with rugulae and punctulate interspaces. Petiolar node a little more sculptured and therefore slightly more subopaque than the postpetiolar node. Base of gaster with longitudinal rugulae of variable length, the longest of which are approximately 0.10 mm but which are best seen only in certain lights. Frontal area, declivity of epinotum, and gaster, rather smooth and shining. Occipital region more shining than the remainder of the head.

Body light brown to brown, the antennae and legs even lighter. Some individuals have a slight infuscation on the dorsal surface of the head and gaster (these may be a little faded due to age).

One of the cotype workers has the entire pronotum covered with very distinct, widely spaced, transverse rugulae, the interspaces punctulate but not causing the surface to be dull enough to keep from shining. Some of the cotype workers have the longitudinal rugulae on the promesonotum rather weak, not widely spaced, and the interspaces enough dull so that the entire promesonotal area is not as shining as in other workers.

The worker of *diecki* is perhaps one of the most highly variable of all our species of *Stenamma*. In Michigan, Minnesota, and southeastern Canada, for example, the workers seem to be characterized in general by their stouter body, lighter color and stouter and more shining postpetiolar node. The postpetiolar node is commonly of a subglobular appearance. In the mountains of Tennessee and North Carolina the worker is unusually large, dark in color, and has a postpetiolar node which is less broad in proportion to its length. The mesoepinotal impression although highly variable in size and

shape is usually very large and distinct. Had I not seen so much variability in the worker of *diecki* throughout its general range and even in individuals from the same colony, I might be inclined to call these two variants subspecies.

Variations in workers other than cotypes from throughout the general range of *diecki* are as follows: Body length from approximately 2.7-3.5 mm; head longer than broad to about as broad as long, with the posterior border straight or weakly emarginate; eye approximately 0.05-0.10 mm in its greatest diameter and usually with 4-6 ommatidia; basal teeth of mandible varying considerably in size and number but commonly with from 4-5, occasionally with 7; mesoepinotal impression highly variable in size and shape, often of a V or U shape and ranging from less than 0.10-0.166 mm in length; epinotal spines highly variable in size and also in the direction which they point, more commonly directed posteriorly than upwards, approximately 0.05-0.10 mm in length; pedicel of the petiole variable in length, often short in appearance; postpetiole generally subcampanulate to subglobose in appearance; rugulae on the pronotum although usually longitudinal in direction, occasionally arched anteriorly, transverse, or irregular in direction; the density of the rugulae also highly variable; body color light brown through reddish brown to almost black but never black, appendages lighter; sides of thorax with the longitudinal rugulae and punctulate interspaces varying a great deal with regard to density and coarseness.

The characters distinguishing the *diecki* worker are the size and structure of the eye, the shining propleuron, mesonotum and postpetiole. Due to its high degree of variability the worker has less good, stable characters than most species of *Stenamma*.

DEALATE FEMALE

Similar to the worker except as described below.

Length 3.7 mm. Eye oblong, 0.2 mm in its greatest diameter and with 14 ommatidia; anterior border of eye less than 0.2 mm from the base of the mandible. Ocelli distinct, each ocellus approximately 0.05 mm in width. Funicular segments 2-6 broader than long; last funicular segment approximately 0.3 mm in length. Thorax 1.25-1.3 mm in length from the anterior border of the pronotal collar to the apices of the epinotal spines; thoracic humeri not well defined, rounded or broadly subangular. Epinotal spines less than 0.10 mm in length and approximately 0.3 mm apart at their apices. In profile, the thorax appears short and rather high with the base of the epinotum sloping and the epinotal declivity almost vertical. Petiolar node, in profile, subangular; postpetiolar node from the same aspect, convex above, but not strongly so.

The longitudinal rugulae on the front of the head rather fine, extending at least to the region of the ocelli. Pronotum coarsely and transversely rugulose, with weakly punctulate interspaces. Mesonotum and scutellum distinctly but less coarsely longitudinally rugulose, with punctulate interspaces. Area between the clypeal carinae, lower half of mesopleuron, and much of the dorsal surfaces of the petiolar and postpetiolar nodes smooth and shining.

Pilosity on dorsal surface of body rather abundant, grayish, composed of erect and also reclinate hairs of variable length, but largely reclinate.

Body light brown or reddish brown; mandibular teeth, eyes, borders of the ocelli and wing articulations dark.

Described from two cotype females.

Females other than cotypes vary largely in the following respects: Body length 3.4-4 mm; thoracic length 1.15-1.4 mm; head 1.12-1.2 times as long

as broad, with the posterior border sometimes feebly emarginate; greatest width of eye 0.17-0.20 mm, with 12-14 ommatidia; mesonotum commonly with a longitudinal carina throughout its center and also with longitudinal rugulae of variable coarseness, the entire surface of the mesonotum usually subopaque; mesopleuron variable in sculpture but usually more or less shining in appearance; epinotal spines ranging from thin to coarse, and small to fairly large, but apparently never over 0.10 mm in length; postpetiole usually longer than wide, sometimes apparently as wide as long, of a sub-campanulate to globular appearance; body light brown or reddish brown to deep blackish brown but not black; antennae and legs often lighter; wings pale to yellowish with usually darker veins and stigma. Venation similar to that of *brevicornis*.

Although highly variable in many respects, the female is fairly constant with regard to a few characters, such as the size of the eye and the number of ommatidia therein, the nature of the sculpturing of the mesonotum and mesopleuron, and the rather smooth and shining dorsal surface of the post-petiolate node.

MALE

Length 2.75-3 mm. Mandible moderately large. Ocelli not large but distinct, not placed on a prominent protuberance above the general surface of the head; anterior ocellus about 0.4 mm from the anterior border of the clypeus. Eye rather large and strongly convex, approximately 0.22 mm at its greatest diameter, the anterior border of the eye about 0.05 mm from the base of the mandible. Antennal scape rather short, about 0.25 mm in length, approximately as long as the combined lengths of the first four funicular segments; the first funicular segment enlarged, subpyriform. Thorax 1.15 mm in length from the anterior border of the pronotal collar to the junction of the thorax with the petiole; widest slightly anterior to the insertion of the wing where it is 0.6 mm; Mayrian furrows present but not always clearly seen in some lights. In profile, base of epinotum meeting the declivity on each side to form an angle or else a very small tubercle. Wings yellowish to sordid in color. In profile, petiole without an especially long peduncle, the ventral surface without a tooth or protuberance; anterior face of node meeting the dorsal surface of the node to form a rather distinct angle. From above, the postpetiole is about as broad as long, somewhat subrectangular in appearance, with the anterior portion of the sides somewhat convergent.

Mesopleuron, dorsal surfaces of petiolate and postpetiolate nodes, and gaster, smooth and shining. Much of head finely punctulate; scutellum with fine, longitudinal rugulae; epinotum punctulate and also finely rugulose; all of these areas subopaque or opaque in most lights.

Body dark brown or blackish brown but not black; mandibles, antennae, legs and apex of gaster lighter.

The description of the male is based on 14 males collected from a colony along with three workers and ten alate females at the Edwin S. George Reserve, Livingston County, Michigan, by Miss Mary Talbot on August 28, 1953, in soil on the north slope of a deep, oak-hickory woods. These individuals bear the No. 53-662.

Variations in individuals from other localities are as follows: Head 1.16-1.2 times as long as broad; anterior ocellus 0.4-0.475 mm from the anterior border of the clypeus; greatest diameter of eye 0.22-0.25 mm; scape 0.23-0.33 mm in length and as long as the combined lengths of approximately the first 4-5 funicular segments; length of thorax 1.1-1.5 mm; greatest width of thorax 0.6-0.75 mm; postpetiole frequently as broad as, or broader than long;

Mayrian furrows and parapsidal sutures present but not always very distinct; prescutum propleuron, and dorsal surface of the epinotum frequently shining; body light brown through brown to black, with the mandibles, antennae, legs and apex of the gaster lighter; wings hyaline to brownish, and of the same venation as in the female.

Type locality.—Of *diecki*, near Yale, British Columbia (Canada). Workers and dealate females collected by Dr. George Dieck; of *impressum*, Richfield Springs (Otsego County), New York. In describing *impressum*, Emery erroneously gave the type locality as Richs Spring, New York and this error was repeated by Creighton in his "Ants of North America."

Location of types.—Of *diecki*, Museo Civico di Storia Naturale, Genoa, Italy, United States National Museum, and the Museum of Comparative Zoology at Harvard College. The holotype worker from which Emery described *impressum* should be in Museo Civico di Storia Naturale but Dr. Delfa Guiglia of this museum writes that she is unable to find the holotype. In the U. S. National Museum there are workers of *impressum* which appear to belong to the original series.

Distribution.—*S. diecki* has been recorded from southeastern and southwestern Canada and most of the United States except the extreme Central States and a few of the Southern States. No doubt the species has a much wider distribution in Canada than present records indicate.

SPECIMENS STUDIED: Of *diecki*, three cotype workers and two dealate cotype females from the Museo Civico di Storia Naturale, Genoa, Italy, one cotype worker from the Museum of Comparative Zoology at Harvard College and one cotype worker from the U. S. National Museum; of *impressum*, two workers in the U. S. National Museum which appear to belong to the original series. The holotype of *impressum* which should be in the Museo Civico di Storia Naturale has apparently been lost. I have also studied 1,279 workers, 26 dealate females, 152 alate females and 96 males from localities other than the type locality.

Mary Talbot (Ent. Soc. Amer. Ann. 44:307, 1951) erroneously recorded as *diecki*, 2 species—*impar* and *meridionale*, both of which had been determined by me. Buren (Iowa State Col. J. Sci. 15:112, 1941) also erroneously recorded individuals of *brevicornis* as *impressum*.

BIOLOGY

This widely distributed species is highly adaptable to various types of ecological habitats. It can be found at altitudes at least as high as 8,000 feet. *S. diecki* appears to be especially common in southern Canada and the most northern tier of our States. In southeastern United States (Virginia, North Carolina, and Tennessee) *diecki* seems to be confined to rather high altitudes. Colonies nest in the soil and in rotting wood. Nests in the soil are usually under cover of stones, logs, humus, moss, etc. Colonies may be found nesting in boggy or swampy areas to rather dry areas and from unshaded conditions through open woods to dense woods. There appears to be only a single queen per colony. The largest colony that has come to my attention contained, on July 31, 97 workers, 98 worker pupae, 1 dealate female, 56 alate females, 28 males and 1 male pupa; the adults alone totaling 182 individuals. Data based on a number of colonies indicate that males and virgin females are produced from midsummer to early fall. Mating flights may take place from spring to fall. In the older colonies it is common for the males and virgin females produced during the current year to remain overwinter in the parental nest and take their nuptial flights in the spring or later the following

year. Nests in the soil are usually shallow, seldom being more than a foot or so from the surface of the soil. There are only a few chambers. The workers are commonly of a timid disposition and on occasion will feign death when disturbed.

Cole (Tenn. Acad. Sci. J. 25:297, 1950) under the name *impressum*, gives an interesting account of the habitats and biology of *diecki*. He studied 18 colonies found in red spruce-balsam fir forest near Newfound Gap, elevation 5,250 feet, in the Great Smoky Mountains National Park, Tennessee. The stands were not dense but the trees close enough to provide continuous dense shade, high soil moisture and low soil and atmospheric temperatures. Underbrush was exceedingly sparse but the ground was covered with decaying logs and a heavy carpet of moss. Each nest consisted of a small superficial chamber in the surface soil just beneath a stone or piece of wood. He found that when disturbed although the workers were sluggish they moved their small batches of brood to cover. Only a single egg mass was noted per nest and this mass contained from 16 to 32 eggs. Eight complete colonies consisting of 12 to 29 workers, a queen and brood were taken to the laboratory for further study. Males emerged from some of the colonies from August 7 to 19, but no females developed in any of the nests. Living collembolans and thysanurans were placed in the nest for food and their internal contents were devoured by the workers.

W. L. Brown and E. O. Wilson, who collected a number of colonies of *diecki* in the White Mountains National Forest of Maine, made the following remarks in a letter to me,

"The *diecki* colonies were taken in rotten wood and under stones at the summit of Evans Notch (a pass through the mountains) and on the east side in both dark beech woods and woods predominantly spruce-fir at somewhat lower altitudes. All localities were shaded and moist; pupae of sexes were present in many nests at this date (mid-August) and eclosed with full pigmentation a few days later in the laboratory. Other White Mountains collections were taken in mixed spruce-fir-birch forest in widely separated localities on the lower slopes on both sides of the Presidential Range. The colonies are quite abundant in many places, though inconspicuous. Few other ants are found in such situations, the most common being *Formica subnuda* Emery, *F. neorufibarbis* Emery, *Camponotus herculeanus* (L.) one or two *Myrmica* spp., and one or two less abundant species.

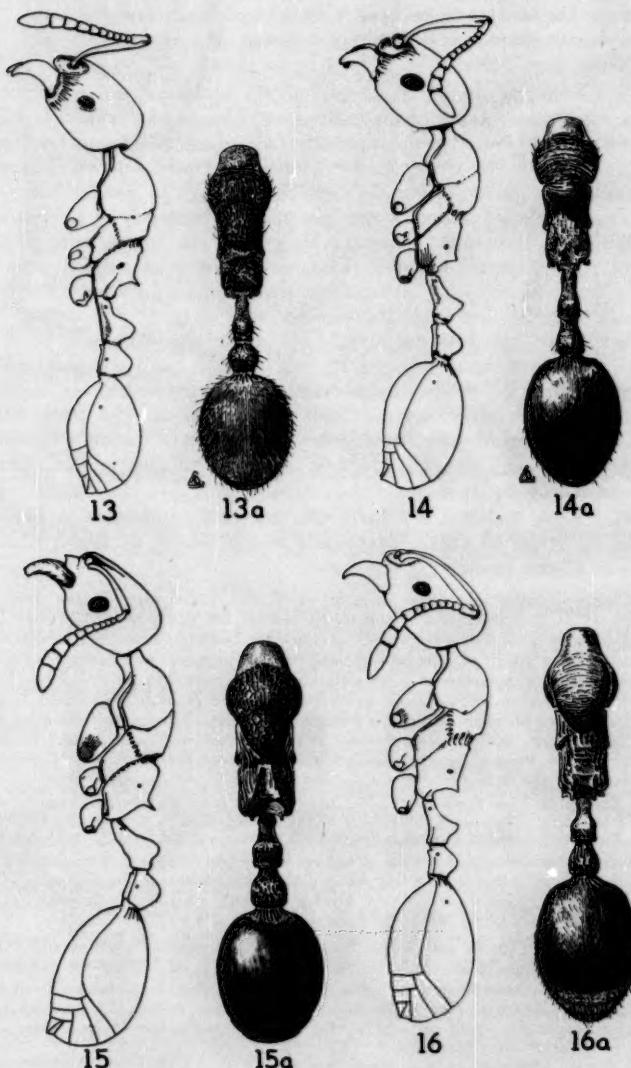
"The *Stenamma* feign death for a short time but are quick and persistent at removing the brood to safety. The nest population of *diecki* are estimated to average about 40 to 60 adult workers each in the White Mountains area. We have not been able to find nests of these or other *Stenamma* species at all in eastern Massachusetts though one can easily find stray workers under stones and in leaf litter during the months at the beginning of the season. We cannot account for the very striking difference in collecting between localities near Boston and those in the White Mountains.

"At Evans Notch Brown and Wilson found larvae of *Stenamma* attached and actually feeding on a dipterous larva which was determined by W. W. Wirth as possibly an empidid. Under the same conditions but in another colony they found what they thought was a *Tomocerus* springtail. Due to the bad condition of the individual when received by Miss Grace Glance she would not confirm the generic determination of the springtail nor even the fact that it was a springtail."

STENAMMA BREVICORNE (Mayr)

Aphaenogaster brevicornis Mayr, 1886, Zool.-Bot. Gesell., Wien, Verh. 36:443, 447-448, worker, alate female. Mayr, 1887, Zool.-Bot. Gesell. Wien, Verh., 37:628, footnote (neoorcticum worker = brevicornis).

PLATE 4



Figs. 13-16.—Lateral view of worker with all segments of legs omitted except the coxae and (a) dorsal view of worker with head and legs omitted. 13. *S. brevicorne* (Mayr); 14. *S. carolinense* M. R. Sm.; 15. *S. meridionale*, n. sp.; 16. *S. foveoloccephalum* M. R. Sm.

Stenamma neoarcticum (Mayr), (Mayr), 1886, Zool.-Bot. Gesell. Wien, Verh. 36:454, worker, (alate female and male misdet.). New Syn.

Stenamma (Stenamma) brevicorne (Mayr), Emery, 1895, Zool. Jahrb. Abt. f. System. 8:299, worker, alate female, male. Forel, 1901, Soc. Ent. Belg. Ann. 45:347.

Stenamma brevicorne (Mayr), W. M. Wheeler, 1903, Psyche 10:166-168, worker. W. M. Wheeler, 1904, Amer. Mus. Nat. Hist. Bul. 20:302 (det. questionable). W. M. Wheeler, 1905, Amer. Mus. Nat. Hist. Bul. 21:382. Gaige, 1914, Mich. Univ., Mus. Zool., Occas. Papers No. 5:3, 9. W. M. Wheeler, 1917 (1916), Conn. State Geol. and Nat. Hist. Survey Bul. 22:585. Davis and Bequaert, 1922, Brooklyn Ent. Soc. Bul. 17:9. W. M. Wheeler, 1926, Ants, p. 150, reprinted, Columbia Univ. Press, N. Y. Bequaert, 1928, in Cornell Univ. Agr. Expt. Sta. Mem. 101:997. Talbot, 1934, Ecology 15:420, 423, 425. Wing, 1939, Ent. News 50:162. Wesson and Wesson, 1940, Amer. Midl. Nat. 24:90, 93. Morris, 1943, Ind. Acad. Sci. Proc. 52:208. Buren, 1944, Iowa State Col. J. Sci. 18:284, worker. Gregg, 1944, Ent. Soc. Amer. Ann. 37:454, 456, 464-465, worker. M. R. Smith, 1947, Amer. Midl. Nat. 37:555, worker. Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:136, worker, female, pl. 17, figs. 1-4 (all castes, also wing). Headley, 1952, Ent. Soc. Amer. Ann. 45:435-442.

Stenamma brevicorne brevicorne (Mayr), M. R. Smith, 1951, in U. S. Dept. Agr. Monogr. No. 2, p. 794.

Stenamma brevicorne diecki var. *impressum* Emery, Buren, 1941, Iowa State Col. J. Sci. 15:112. (misdet.)

WORKER (pl. 4, figs. 13, 13a)

Length 2.7-3.8 mm. Funicular segments 2-6 as broad as, or broader than long; the four apical segments of the funiculus distinctly enlarged but not forming a well defined club; the length of the club exceeding the length of the remainder of the funiculus. Eye moderately large for a *Stenamma*, oblong, usually with approximately 8-10 ommatidia in its greatest diameter. The promesonotum, in profile, forming a rather long, uninterrupted arch in which the anterior half of the arch is distinctly more convex than the posterior half. Mesepinotum impression usually strong and approximately twice as long as deep. Epinotum lower than the mesonotum and usually with a prominent, transverse welt near the base following the mesepinotum impression. Base and declivity of the epinotum meeting to form a pair of short, but distinct, tuberculate spines which are approximately one-fourth to one-third the length of the base of the epinotum. Petiolar node viewed posteriorly with dorsally converging sides and truncate or feebly rounded superior border. Postpetiolar node viewed from above, stout, of variable shape, usually subspherical but occasionally subrectangular or transversely elliptical.

Frontal area and much of the clypeus smooth. Frontal region bearing fine, longitudinal and posteriorly diverging striae. Cheeks mostly longitudinally rugulose-punctate. Promesonotum usually largely, longitudinally rugulose, with the anterior border of the pronotum transversely rugulose. Dorsal surface of the epinotum with variable sculpture but quite commonly irregularly rugulose or rugulose-reticulate. Sides of thorax mostly rather coarsely, longitudinally rugulose with the exception of the lower part of the mesopleuron which is commonly reticulate-punctate. Base of gaster with distinct but short, longitudinal rugulae which are apparently never as long as the postpetiole. Petiolar and postpetiolar nodes mostly punctate or rugulose-punctate.

Head (with the exceptions of the mandibles, clypeus and frontal area), thorax, petiole and postpetiole, subopaque. Gaster smooth and shining. Propleuron occasionally somewhat shining.

Body with rather abundant, suberect to erect, grayish or light yellowish hairs of variable length. Head, and especially the gaster, usually more hairy than the thorax. Hairs on appendages abundant but not always very closely appressed.

Head, thorax, petiole and postpetiole dark brown; antennae and legs light brown or yellowish brown. Gaster brown or blackish with the apex and the base lighter thus causing the dark area to appear as a more or less distinct, transverse band.

The head varies very noticeably in shape; with some individuals it is slender, very distinctly longer than broad whereas in other individuals the

head is almost square but never quite as broad as long. The number of ommatidia in the greatest diameter of the eye is also subject to considerable variation, usually there are approximately 8-10 but one individual had only 4 or 5. Although it is common for the epinotum to bear a transverse welt near the base, the welt may be obscure or even lacking in some individuals. The postpetiolar node although usually subspherical may sometimes be transversely elliptical or even subrectangular. The sculpture on the promesonotum is usually largely longitudinally rugulose, occasionally there are individuals in which the rugulae have an arched or oblique trend or even an irregular, indescribable pattern. The color of the head, thorax, petiole and postpetiole is quite commonly reddish brown but often may be a light brown. Although the gaster is usually darker in the middle than at the base and tip there are individuals in which the base may be as dark as the median area.

The worker of *brevicornis* may be distinguished by its moderately large eye, which usually bears 8-10 ommatidia in its greatest diameter; the strong mesoepinotal impression which is frequently twice as long as deep; base of epinotum usually with a transverse welt following the mesoepinotal impression; the distinct spines which are approximately one-fourth to one-third the length of the base of the epinotum; petiolar node subconical, when viewed from behind; postpetiolar node, from above, stout, as broad as, or broader than long; head, thorax, petiole and postpetiole subopaque; promesonotum largely coarsely longitudinally rugulose; body usually brown with the gaster light at the base and apex and darker medianly.

ALATE FEMALE

Similar to the worker except as described below.

Length 3.4-4.2 mm. Ocelli small, yellowish, not noticeably protruding above the general surface of the head, the anterior ocellus located from 0.3-0.4 mm posterior to the frontal area. Greatest diameter of the eye ranging from 0.2-0.25 mm and with 14-18 ommatidia. Antennal scape failing to attain the posterior border of the head by its greatest diameter or less, funicular segments 2-7 as broad as, or broader than long; last segment of the club not as long as the combined lengths of the three preceding segments. Thorax 1.35-1.6 mm in length from the anterior border of the pronotal collar to the apices of the epinotal spines, widest anterior to the articulations of the anterior wings where it measures 0.65-0.75 mm. Epinotal spines, in profile, variable in size and shape, usually stout and prominent and ranging from 0.10-0.15 mm in length; from above, the spines are approximately one-fourth to one-third as long as their interapical distance. Anterior wing grayish to yellowish depending upon the light, normally containing a closed cubital and a closed discoidal cell and a well developed stigma; without vein r_m but with Mf^3 present (Plate 1, fig. 2), occasionally one or both of the anterior wings may have a partly or fully closed second cubital cell. Mf^2 is seldom absent but an occasional individual may lack this vein in one or both anterior wings. Upon infrequent occasions the discoidal cell may be only partly closed in one or both wings. Petiolar peduncle, in profile, often rather short and stout, the node subangular, slightly higher than long; postpetiole, in profile, approximately as high as long. Postpetiolar node, from above, convex, wider than long.

Scutellum and much of the mesonotum largely longitudinally rugulose-punctate. Pronotum, exclusive of the collar, largely transversely rugulose-punctulate. Area above the epinotal spines transversely rugulose with punctate interspaces, the sculpturing often extending well down below the spines, occasionally however the area below the spines may be smooth or almost so.

Head, thorax, petiole, and postpetiole ranging from a light brown or reddish brown through dark brown to almost blackish brown.

Variation occurs mostly in the length, proportion, and color of the body. The variation of the wings is apparently less than other types of variation; it commonly consists in a partly or fully closed extra cubital cell, lack of M_3 or in the presence of a partly closed discoidal cell.

The female can be distinguished from that of other forms by its large size; stout body; nature of the wing venation; sculpturing of the thorax (especially of the sides and posterior portion); rather prominent and stout epinotal spines; and the shapes of the petiolar and postpetiolar nodes, as well as the nature of their sculpturing.

MALE

Length 3.3-5 mm. Ocelli distinct but not prominent or protruding above the general surface of the head, the anterior ocellus approximately 0.05 mm in width and located 0.2-0.25 mm posterior to the frontal area. Frontal area small but distinct, longer than broad. Frontal carinae short, 0.15-0.20 mm in length, subparallel, with scarcely any lobes. Eye large and prominent, 0.25-0.30 mm through its greatest diameter. Antennal scape (excluding the pedicel) approximately 0.28-0.37 mm in length, approximately as long as the combined lengths of the first four to six funicular segments; last funicular segment approximately as long as the combined lengths of the two preceding segments. Middle of the dorsal surface of the clypeus with a flattened area or impression that is longitudinal in direction. Mandible rather small, subtriangular. Thorax 1.1-1.5 mm in length from the anterior border of the pronotal collar to the apices of the epinotal spines, greatest width 0.6-0.75 mm just anterior to the articulations of the anterior wings. Mayrian furrows well developed, the parapsidal sutures present but best seen only in certain lights. In profile, base of epinotum depressed or flattened but the surface not horizontal, the base and declivity meeting on each side to form a broad tubercle or angle. Petiole, in profile, pedunculate, with a low not strongly convex node, which is approximately as long as the peduncle. Postpetiole, in profile, larger than the petiolar node, approximately as high as long. From above, postpetiolar node as broad as, or broader than long, usually with the appearance of being broader than long.

Head varying from rather densely and finely punctulate to reticulate-punctulate, the front with fine longitudinal striae; base of epinotum and sides of the petiole and postpetiole largely punctulate. Mesonotum and scutellum largely longitudinally rugulose-reticulate and punctate or punctulate, the area between the Mayrian furrows less heavily sculptured and therefore more shining than the mesonotum. Mesopleuron usually more weakly sculptured than the side of the epinotum which is irregularly rugulose-reticulate and punctulate. Gaster, and dorsal surface of the postpetiolar node, smooth and shining.

Pilosity light yellowish or grayish, moderately abundant, consisting of hairs of variable length which are suberect to erect.

Body brown to brownish black; mandibles, antennae, legs and apex of gaster light brown to yellowish, usually distinctly lighter than the remainder of the body.

Variations occur in the size of the male as well as in the proportions of the body. Individuals have been noted with the following abnormalities in the venation of the anterior wings: one or both wings with either a partly or else a fully developed extra cubital cell; also one or both wings lacking a closed discoidal cell or else having only a partly closed discoidal cell.

The male is distinguished from that of other species largely by the shape of the epinotum as well as the nature of the wing venation.

Type locality.—Virginia. Described by Mayr from workers and alate females collected by Theodore Pergande from beneath a stone in a locality presumably near Washington, D. C.

Location of types.—The Gustav Mayr collection in the Naturhistorisches Museum in

Vienna, Austria. A cotype worker and female are in the U. S. National Museum as well as two workers and four females apparently belonging to the original series.

Distribution.—This species is distributed from at least Nova Scotia, Quebec, and Ontario south to Virginia and west to Nebraska and Minnesota. W. M. Wheeler records *brevicornis* from workers collected at Friday Harbor, Washington, by Trevor Kincaid and from a single worker collected from the north fork of the Swannanoa in North Carolina presumably by William Beutenmueller. Although I have not seen the specimens from these two localities, I feel quite positive that the Friday Harbor individuals were misdetermined and that the North Carolina record is questionable since no one else has recorded or found *brevicornis* in that State. Wheeler also misdetermined nine males of *diecki* as *brevicornis* which were collected at Dikes Peak, Mt. Desert Region, Maine, on October 2, 1934, by A. E. Brower. Ames and Arnold Park, Iowa individuals of this ant were also misdetermined by Buren (Iowa State Col. J. Sci. 15:112, 1941) as *impressum*.

SPECIMENS STUDIED: Six cotype workers and two alate females from the Naturhistorisches Museum, Vienna, Austria, a cotype worker and alate female in the U. S. National Museum as well as two workers and four females apparently belonging to the original series; also 586 workers, 4 dealate females, 205 females and 214 males from localities other than the type locality.

BIOLOGY

S. brevicorne is not only one of the most widely distributed but the oldest and perhaps best known of our North American species of *Stenamma*. Although apparently preferring to nest in wooded areas, the species is also found in meadows and other places. It usually nests in moderately dense to dense woods of such composition as maple, mixed oaks, oak-maple, red and white oaks, and beech-maple. Here the ants more commonly nest in the soil under stones, logs, humus, moss or other debris, as well as in the rotting wood of logs and stumps. Colonies are small, consisting of only a few dozen to a hundred or so adult individuals. The largest that has come to my attention was found at Tiffin, Ohio, on August 21, 1948, by Talbot and Headley and was composed of 105 workers, 8 alate females, and 12 males. Although no one has made a detailed study of *brevicornis*, random observations indicate that this species is timid and sluggish, subterranean or hypogaeic. The workers are undoubtedly carnivorous, but may also be predaceous. Wheeler, so far as I am aware, was the first individual to advance the theory that, in some colonies at least, winged females and males overwinter in the parental nest, these sexual castes having been produced from late summer to early fall. None of the evidence I have seen disproves this, but no doubt the age of the colony has a great deal to do with whether or not sexual castes can be produced. As the colonies are not large, it is likely that there is only one mother queen per colony. This also seems to be the case in many, if not most of our own species. The overwintering sexual castes apparently start emerging from the parental colony in spring or early summer of the following year. It is believed that it is then that mating and the forming of new colonies are started. H. V. Weems, Jr., captured a copulating male and female on May 14, 1950. Since alate females have been captured at light traps and males taken while flying at dusk, it appears that both castes fly freely at night, like many other ants. Although altitudinal records are lacking for *brevicornis*, it appears that this form lives in low lands or areas of only moderately high elevation.

Stenamma meridionale, n. sp.

Stenamma diecki Emery, Talbot, 1951, Ent. Soc. Amer. Ann. 44:307 (part). Misdet.

WORKER (pl. 4, figs. 15, 15a)

Length 4 mm. Last funicular segment 0.35 mm in length, longer than the combined lengths of the two preceding segments. Eye oblong, placed a little more than its greatest diameter from the base of the mandible, the greatest diameter less than 0.2 mm and composed of 9 or 10 ommatidia. Thorax 1.4 mm in length measured from the anterior border of the pronotal collar to the apices of the epinotal spines; with rather rounded or subangular humeri; widest through the prothorax (0.6 mm), narrowest through the epinotum (0.45 mm). In profile, with a very pronounced mesoepinotal impression which is approximately 0.15 mm in its greatest length and slightly more than 0.05 mm at its greatest depth. Base of epinotum distinctly inclined posteriorly, approximately 0.3 mm in length, the base of the epinotum meeting the declivity to form a pair of well developed, long, finger-like spines which are between 0.05-0.10 mm in length, and are directed posteroventrally and somewhat laterally. From above and somewhat behind, the petiolar node appears compressed anteroposteriorly and has subparallel sides and a weakly emarginate but not sharp, transverse, superior border. Postpetiole, from above, subcampanulate, scarcely longer than broad. Gaster, from above, oblong or subelliptical, without basal humeri.

Head with rather coarse, distinct sculpturing; front of head bearing a number of longitudinal striae which extend to approximately the posterior border of the head; much of the remainder of the head with rugulose-reticulate to reticulate sculpturing, the interspaces punctulate. Thorax, from above, with rather coarse and somewhat widely spaced rugulose-reticulate sculpturing, some of the rugulae on the pronotum, at least, with a longitudinal trend; side of thorax somewhat similarly sculptured except that perhaps the ventral half or more of the mesopleuron is largely reticulate. Pedicel and anterior face of petiolar node punctulate, the dorsal and posterior surface of the node rugulose-punctate; postpetiole sculptured somewhat similarly. Basigastric striae more than 0.1 mm in length. Frontal area, epinotal declivity and gaster smooth and shining. Most of the head, the thorax, petiole and postpetiole subopaque (slightly shining however in some lights).

Hairs moderately abundant, yellowish, of variable length, largely reclinate to suberect; apparently longest on the clypeus and the front of the head.

Body dark brown, to some extent with a blackish cast; anterior portion of the head, antennae, legs and apex of gaster a much lighter or yellowish brown.

Paratype workers vary from the holotype worker in the following characters: Body length 3.4-4 mm; head 1.10-1.12 times as long as broad with the posterior border straight or broadly and almost imperceptibly emarginate; length of thorax 1.25-1.4 mm; greatest width (through pronotum) 0.5-0.6 mm; narrowest width (through epinotum) 0.375-0.45 mm; last funicular segment 0.3-0.35 mm in length and longer than the combined lengths of the two preceding segments; the 1st, and 7th through 11th funicular segments, longer than broad; eye with 8-10 ommatidia in its greatest diameter; mandible usually with five basal teeth but occasionally as many as six teeth; superior border of petiole straight or feebly emarginate; postpetiole, from above, almost as broad as long to 1.2 times as long as broad; head, thorax, petiole and postpetiole from light brown to dark brown with a decided blackish cast.

Workers other than paratypes show the following variations: Body length 2.8-4 mm; head 1.10-1.23 times as long as broad; thoracic length 1.1-1.4 mm; greatest prothoracic breadth 0.45-0.60 mm; narrowest breadth of thorax (through epinotum) 0.35-0.40 mm; mesoepinotal impression 0.1-0.15 mm in length and usually about 0.05 mm in depth; last funicular segment 0.3-0.35 mm in length; greatest diameter of eye 0.1-0.15 mm with 6-10 ommatidia; petiolar node from above and behind with subparallel to dorsally converging

sides and with the superior border of the node straight or rounded; sculpturing of head not always coarse; epinotal spines from tuberculiform to slender, digitiform; epinotum occasionally with a transverse welt at the base; pronotum and mesonotum often with well defined and rather broadly spaced longitudinal rugulae, the interspaces of which are either smooth or finely punctulate; body varying from light reddish brown to dark reddish brown, the anterior portion of the head, appendages and apex of the gaster usually lighter.

The worker can be distinguished by the following characters: Large size, 3.4-4 mm; large eyes, which have 8-10 ommatidia in their greatest diameter; pronounced mesoepinotal constriction, which is often as much as 0.15 mm in its greatest length and from 0.05 to almost 0.10 mm in depth; the posteriorly sloping base of the epinotum; the long, finger-like epinotal spines; and the anteroposteriorly compressed petiolar node, which when viewed from above and behind is subrectangular and has a straight or weakly emarginate superior border.

DEALATE FEMALE

Length 4.6 mm. Similar to the worker except in the following respects: Head 1.08 times as long as broad; anterior ocellus located approximately 0.4 mm back of frontal area; length of thorax 1.7 mm; greatest breadth of thorax (through the mesonotum anterior to the wing insertions) 0.85 mm; narrower breadth (through the epinotum) 0.55 mm; greatest diameter of eye between 0.25-0.30 mm with approximately 18 ommatidia; epinotal spines well developed, approximately 0.10 mm in length, stout, with blunt apices, from above, at least three times as far apart at the apices as are the length of the spines; mesonotum with well spaced, longitudinal rugulae; base of epinotum with coarse, transverse rugulae; sides of prothorax and epinotum largely with coarse, longitudinal rugulae with punctate interspaces, most of the mesopleuron largely smooth and shining.

Females other than the paratype show the following variations: Body length 3.9-4.6 mm; head 1.08-1.14 times as long as broad; anterior ocellus located from 0.35-0.40 mm back of frontal area; length of thorax 1.35-1.7 mm; greatest breadth of thorax 0.7-0.85 mm; narrowest breadth of thorax 0.40-0.55 mm; greatest diameter of eye 0.2-0.3 mm; with 14 to 18 ommatidia therein; epinotal spines 0.25-0.35 mm apart at their apices; mesopleuron usually more smooth and shining than the remainder of the side of the thorax, although it may be sculptured somewhat; dorsal surface of body often infuscated, with the anterior portion of the head, the appendages and apex of gaster, and some scattered areas on the mesonotum lighter.

The female is distinguished from that of other species largely by the following characters: Large size, large eyes with 18 ommatidia in their greatest diameter; nature of the sculpturing of the body; the large and characteristic shaped epinotal spines and the shape of the petiole and postpetiole, especially the former.

Type locality.—Droste Woods, St. Charles County, Missouri. Described from individuals collected from two colonies by Mary Talbot. The holotype and 15 paratype workers from colony No. 48-2 collected 11-10-48 and a wingless female and 11 paratype workers from colony No. 52-12 collected 10-6-52. All of these have been placed in the U. S. National Museum under U.S.N.M. No. 62392.

Distribution.—Va., Mo. and Ill. south to S. C. and Ark. The most northern locality from which this species has been collected is Oakwood, Vermilion County, Ill., which is slightly above the 40th degree of latitude.

SPECIMENS STUDIED: In addition to types, 77 workers and five dealate females from localities other than the type locality.

Three workers and one dealate female of *meridionale* from the Gustav Mayr collection were found erroneously mixed with types of *brevicorne*.

BIOLOGY

The only collections of *meridionale* made directly from colonies were those of Mary Talbot in the Droste Woods in St. Charles County, Missouri. She described the woods as a small, mixed oak-hickory woods, with large red and white oaks predominating. There was a great variety of other trees such as linden, elm, sycamore, maple, and sassafras. The collections were made in a pawpaw thicket occupying a gentle slope from a ridge to a small stream in the center of the woods. The trees overhead allowed moving patches of sunlight but did not form the continuous deep shade of beech-maple woods. There were scattered shrubs of buck brush, elderberry, sumach, etc., with the herb layers consisting of spring blooming flowers such as spring beauty, mandrake, dentura, and red trillium. The ground cover had a fairly heavy leaf covering mixed with a litter of twigs, acorns, hickory nuts and decaying branches. The soil was very dark and loose for three or four inches, then it became progressively compact and light colored until below six or seven inches it was a very hard-packed clay. Colony 48-2 was collected November 10, 1948, from two chambers in which the ants were hibernating in hard clay in depths of 10 and 15 inches. This colony was found when the air temperature was 43° F and the soil temperature 52° F. In the 10-inch chamber both workers and larvae were found, in the 15-inch chamber only a few workers. Although the ground was dug to a depth of 21 inches, no other immature stages or adults were found. The total content of the nest was 19 workers and 36 medium to large larvae, but no pupae, females, or males. This may not have represented the entire colony. The second colony, 52-12, was found October 6, 1952, in a chamber 13 inches deep which looked like a horizontal crack in the dry, hard clay. There had been no cold weather and the ants were still foraging in the woods. The air temperature at this time was 73° F, and the soil temperature 58° F. From the chamber were taken 11 workers and one dealate female, four larvae but no eggs, pupae, winged females or males.

In localities in other states where collections were usually made with Berlese funnel, single collections usually produced only from 1-13 workers with occasionally a dealate female. These individuals were largely taken from leaf mould, ground cover or top soil, mostly, if not entirely, in the woods. At this time we do not know the maximum size of colonies, the diversity of the nesting habits nor the month or months of the year in which males and winged females are produced.

STENAMMA CAROLINENSE M. R. Smith

Stenamma carolinense M. R. Smith, 1951, Wash. Ent. Soc. Proc. 53:156-158, 2 figs., worker.

WORKER (pl. 4, figs. 14, 14a)

Length 3.8-4 mm. Eye subelliptical, extremely large for a *Stenamma*, with about 10-

12 well defined ommatidia in its greatest diameter which is approximately 0.2 mm. All funicular segments as long as broad or longer than broad, the last four funicular segments forming a rather indistinct club. Thorax, in profile, with the promesonotum rather uniformly convex up to the point where the posterior part of the mesonotum forms a more or less straight incline into the mesepinotal impression. Mesepinotal impression strongly developed, apparently more than twice as long as deep. Epinotum, in profile, with a straight, subhorizontal base, which is separated from the declivity by a pair of extremely short, blunt, tuberculate spines, the spines at best not more than 0.2 the length of the base of the epinotum. Petiolar node, in profile, distinctly angular; from above and behind, slender, subrectangular to subconical, with straight or weakly rounded superior border. Postpetiole, from above, subcampanulate, apparently longer than broad. Base of gaster with longitudinal rugulae which are apparently less than 0.2 mm in length.

Cheeks and front of head with longitudinal rugulae; much of the remainder of the head rugulose-reticulate with punctate interspaces. Promesonotum largely smooth and shining, but also with fine, transverse rugulae, which in some lights are poorly defined. Mesopleuron and side of epinotum with rather coarse, longitudinal rugulae. Rear of petiolar node largely punctulate. Petiolar node mostly smooth and shining, even though bearing a small number of longitudinal rugulae.

Body clothed with suberect to erect grayish or light yellowish hairs, those on the head and gaster apparently denser than on the thorax.

Body light brown to brown, with the gaster scarcely darker than the remainder of the body. Vertex of head infuscated.

Very little variation has been noted in the types. The proportions of the head range from approximately 1.1 to 1.2 times as long as broad; the greatest diameter of the eye is approximately 0.2 mm and has 10-12 ommatidia; the petiolar node viewed from above and behind is slender, subrectangular to subconical; the color of the body varies from light brown to brown with scarcely darker gaster, on the paratype however, the median area of the gaster is very slightly darker than the base and apex.

The characters which distinguish the worker of *carolinense* are: The large size (3.8-4 mm); the unusually large eye for a *Stenamma*; weakly bicarinate clypeus; pronounced mesepinotal impression; straight, subhorizontal base of the epinotum; extremely short, blunt, tuberculate spines; subcampanulate postpetiole; the rather smooth and shining promesonotum with fine, transverse rugulae; the light brown to brown body, with scarcely darker gaster.

Type locality.—A peach orchard on U. S. Highway 1, approximately 1 mile north of Hoffman, Richmond County, North Carolina. Described from two workers collected February 10 and 11, 1937, by William F. Turner from sparsely vegetated sandy soil.

Location of types.—A holotype and paratype worker in the U. S. National Museum.

Distribution.—Known only from the types.

SPECIMENS STUDIED: The holotype and paratype worker.

STENAMMA FOVEOLOCEPHALUM M. R. Smith

Stenamma foveolocephala M. R. Smith, 1930, Ent. Soc. Amer. Ann. 23:564-565, worker.

Stenamma foveolocephala M. R. Smith, M. R. Smith, 1931, Ent. News 42:17.

Stenamma foveolocephalum M. R. Smith, M. R. Smith, 1947, Amer. Midl. Nat. 37:555, pl. 6, fig. 22, worker. M. R. Smith, 1951, in U. S. Dept. Agr. Monogr. No. 2, p. 795.

Stenamma foveolocephalum M. R. Smith, Creighton, 1950, Harvard Univ., Mus. Comp. Zool. Bul. 104:136-137, worker.

WORKER (pl. 4, figs. 16, 16a)

Length 3.6-3.9 mm. Eye subelliptical, rather large for a *Stenamma*, with its greatest diameter approximately 0.15 mm and composed of seven or eight ommatidia. Second to sixth funicular segments as long as broad or longer than broad; the last funicular segment not as long as the combined lengths of the three preceding segments. Thorax, in profile, with the promesonotum more convex in the anterior than the posterior half. Mesoepinotal impression pronounced, approximately twice as long as deep. Base of epinotum sloping posteriorly to meet the declivity and forming two distinct tuberculate but acutely pointed spines which are about 0.16-0.2 the length of the base of the epinotum. Petiolar node, from above and behind, subconical, with weakly emarginate superior border. Postpetiole, from above, subcampanulate, approximately as broad as long but with the appearance of being longer than broad. Base of gaster with short, (0.10 mm or less) but in some lights, distinct longitudinal rugulae.

Mandibles rugulose-punctate, the punctures large, coarse and scattered. Cheeks with coarse longitudinal rugulae. Front with posteriorly divergent, longitudinal striae. Much of the dorsal surface of the head coarsely reticulate-punctate. Dorsum of the thorax, especially the promesonotum, rather coarsely and transversely rugulose-reticulate. Sides of thorax with coarse, longitudinal rugulae. Petiolar and postpetiolar nodes rather coarsely rugulose-reticulate. Frontal area, epinotal declivity and gaster smooth. The body and appendages shining in most lights.

Hairs moderately abundant, light yellowish or grayish, suberect to erect.

Body, exclusive of the gaster, dark reddish brown. Vertex of head infuscated. Gaster brownish except at the base and apex. Appendages lighter than the remainder of the body.

The worker of this form can be distinguished by: Its large size (3.6-3.9 mm); rather large eye for a *Stenamma*; pronounced mesoepinotal impression; the two distinct, tuberculate spines which are acutely pointed and about 0.16-0.20 the length of the base of the epinotum; the subcampanulate postpetiole; sculpturing of the dorsal surface of the thorax, especially of the promesonotum; largely rugulose-reticulate petiolar and postpetiolar nodes, and the color of the body.

Type locality.—Southern slope of a thinly wooded hillside, two miles south of Ackerman, Mississippi. Described from two workers collected from sandy soil by M. R. Smith.

Location of types.—One cotype worker in the U. S. National Museum which I hereby designate as the lectotype. A second cotype worker in the collection of the Department of Entomology of the Mississippi State College has apparently been lost.

Distribution.—Known only from types.

SPECIMENS STUDIED: A single lectotype worker in the U. S. National Museum.

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Notes on Zenker's Organs in the Ostracod *Candona*

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Male ostracods of *Candona* and other genera of the family Cyprididae have paired ejaculatory apparatus, commonly called Zenker's organs. These distinctive, voluminous organs lie in the posterodorsal part of the body, one on each side (fig. 8). Each Zenker's organ consists of a central tube, several wreaths of chitinous spines, numerous tiny muscles, and a surrounding cylinder of epithelial tissue. The central tube is composed of epithelium reinforced with numerous hollow chitin rings, closely spaced but allowing the organ to be shortened by contraction of the muscles. Several wreaths of radiating chitin spines are attached to the central tube and laced together by an intricate set of very small muscles. The front and rear wreaths, which form the two ends of the cylindrical organ, are more complex than the others and have funnel-shaped indentations. The central tube is part of the vas deferens. In copulation, the muscles rhythmically contract in sequence to draw the spines together, shorten the central tube, and force the very long spermatozoa through the organ and out of the penis.

The male sex system, of which the Zenker's organs are integral parts, is rather complex in cypridid ostracods. Each half of the system is complete and lies on one side of the median plane; it is approximately a mirror image of the half on the opposite side, but is in no way connected to it.

To show the relationship of Zenker's organ to other male sex organs, one half of the system is here described briefly. The four testes lie in the hypodermis, a thin flap of tissue which spreads out from the side of the body and lines the valve. They are parallel and, from their syncytia in the posterior part of the hypodermis, curve downward, forward, and upward (fig. 9). At their entrance into the body, the testes unite to form a vas deferens, which has a devious circuit. The vas deferens re-enters the hypodermis at the side of the forehead, curves parallel to the free edge of the valve, and ends blindly in the posterodorsal region. Upon reaching the blind end, spermatozoa reverse their direction and retrace their route to the ventral region where they enter a second branch of the vas deferens, which parallels the first along the anterior margin of the hypodermis (fig. 9). The vas deferens then extends to the rear of the body, loops back and forth a few times, encircles the Zenker's organ, and enlarges to form a seminal vesicle. Zenker's organ lies immediately behind the seminal vesicle (figs. 8-9). It surrounds a short section of the vas deferens. From the rear of the organ a very narrow tube leads into the intricate penis, in which it makes a more or less S-shaped circuit, marked by several enlargements. It terminates at the tip of the inner lobe of the large penis (fig. 9).

PREVIOUS WORK

Although Zenker's organs have been known for more than a century, there have been many conflicting interpretations of their structure and function. Several statements that were true were denied by later authors. Only the

highlights of the published accounts and selected quotations are given here on the important discoveries and ideas concerning these unusual organs.

Perhaps the first mention of these organs was by Ramdohr (1808), who mentioned "längliche, dunkle, der Länge nach gefranzte und in eine weite durchsichtige walzenförmige Membran eingeschlossene Körper." Much of Ramdohr's work was later discounted because he described both male and female organs as though they were from one animal. If we regard his observations as compilations from many specimens, however, it becomes clear that he was the first to isolate and describe many anatomical features of ostracods. His Plate 3, fig. 10, leaves little doubt, at least in my mind, that he actually saw these organs, although he showed them connected to the third thoracic legs.

Zenker was the first worker to investigate in detail the male and female sex systems in ostracods and the first to give a lucid account of the organs that bear his name. In 1850 he called each of the organs a "glandula mucosa" in the belief that it supplied a secretion to the penis. In his Plate 5, fig. 1, he illustrated the vas deferens and Zenker's organ independently leading into the penis. Despite his misinterpretation of the function and anatomical connection of the organ, Zenker gave an excellent description. He discovered the central tube, seven wreaths of radiating chitin spines, and the outer cylinder. He wrote (p. 196):

Seine Axe wird von einem engeren Cylinder gebildet, von dem ein Ausführungsgang zum Penis führt. Von der Axe aus strahlen an den äusseren Cylinder 7 scheibenförmige System von Borsten, in gleichen Abständen. Das erste und letzte, die die beiden Cylinder-Grundflächen bilden, sind aus mehreren Schichten von Borsten zusammengesetzt, die inneren 5 sind einfacher gebaut.

In 1853 Lilljeborg called the organ a "materia carnosa." He remarked that the "glandula mucosa" of Zenker did not have a separate duct leading into the penis but that the vas deferens passed through it. Furthermore, he noted that the larger cylinder contained muscles instead of glands.

In his comprehensive monograph of 1854, Zenker added to his previous description of the organ that the inner cylinder consisted of chitin rings. Evidently Zenker was unaware of Lilljeborg's publication of the preceding year, for he did not comment on it. He referred to the organ as "Schleimdrüse (glandula mucosa)" and reiterated his belief that it contained glandular cells. Zenker saw stripes parallel to the axis, which he interpreted as chitin; there can be little doubt that they were muscles.

Leydig (1860) at first thought the organ, which he called an "accessorische Geschlechtsdrüse," might be similar to the accessory sex glands in some insects, in which the one-celled glands open through chitin ducts into a central chitin canal. However, he discounted this theory when he found muscles but no glands in the organ. He did not suggest a specific function.

Weismann (1880), in his very brief but informative paper on parthenogenesis in Cyprididae, was the first to decipher the use of the organs. He concluded that each was a remarkable kind of ejaculatory apparatus and part of the vas deferens. He stated (p. 84):

So ist die kolossale sog. "Schleimdrüse," welche Zenker bei den Männchen der Cypriden beschrieb, keine Drüse, sondern ein höchst merkwürdiger Ejaculationsapparat. Er hängt nicht seitlich dem Vas deferens an, sondern ist in den Verlauf desselben eingeschaltet.

In 1880, the year that Weismann's article appeared, G. Wilhelm Müller followed the interpretation of Zenker and called the organs "Schleimdrüse." In 1884, Müller again expressed his belief that they were mucous glands, and emphatically stated that Weismann was incorrect. He seems to have had some doubt about the position of Zenker's organ in the male reproductive system, for he said that the relationship of the vas deferens to the penis was not known with certainty although the "Schleimdrüse" emptied through the penis.

Rehberg (1884) concluded the organ was too rigid to act as an ejaculator, and suggested that it was an armored seminal receptacle for protection of the spermatozoa against pressure exerted by closing of the valves.

Most writers after Rehberg have agreed with Weismann. Nordqvist (1885) described details based on sections through the "Ejakulationsapparat." Stuhlmann (1886) gave a full and essentially correct account of the male sex system, and also referred to the organ as an ejaculation apparatus. Schwarz (1888) believed that it functioned as a "Sämenpumpe" in "*Cyprois*" (*Notodromas*) and probably in *Candona*, but that in other ostracods it was an incompressible vestigial organ in which the epithelium produced a secretion. He thought in *Notodromas* the forked spines served to lengthen the central tube and the muscles to shorten it again.

In 1889 Müller called it a "Ductus ejaculatorius." In 1894 he apologized for his 1880 and 1884 articles, stating that they served only to warm up the error of Zenker. He described in detail the construction and action of the organ in several groups of ostracods.

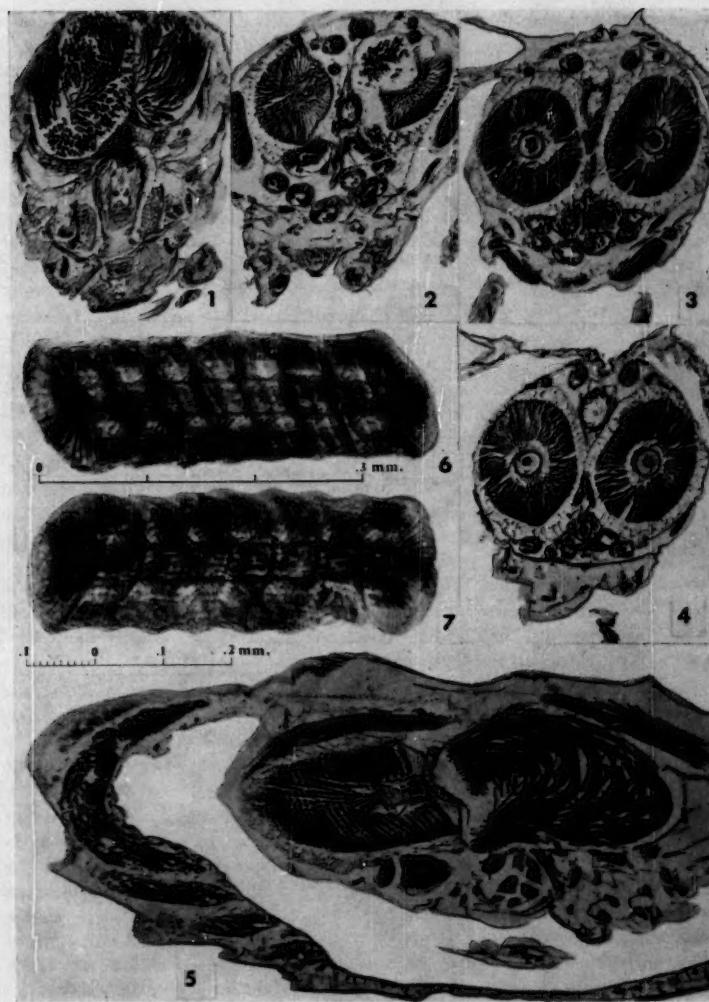
Vávra (1891, p. 23) gave the organ its common name: "Als 'Zenker'sche Organ' bezeichne ich jenen Theil des Samenleiters, den Zenker als 'glandula mucosa' beschrieb. . ." He agreed with Schwarz that it was a functional ejaculator in *Notodromas* and vestigial in other genera.

Claus (1890) endorsed the conclusions of Weismann and his students, Stuhlmann and Nordqvist. He later (1893) referred to the organ as an ejaculation apparatus, and noted correctly that in *Candona* the organs are related to dimorphic differences in shape of the valves. Later writers did not add to our understanding of the Zenker's organs, and simply reviewed the old literature.

In zoological literature there are four statements about Zenker's organ which have been generally accepted, but which I have found to be false or to have exceptions. These statements express (1) that the enlargement of the vas deferens, which I call the seminal vesicle, is not immediately in front of Zenker's organ, (2) that spermatozoa do not lie in Zenker's organ except during ejaculation, (3) that only one spermatozoon enters Zenker's organ at a time, and (4) that each organ in ostracods of the genus *Candona* has seven wreaths of chitinous spines.

SEMINAL VESICLES

Zenker noted an enlargement of the vas deferens in 1850. He stated (p. 195), "Die 5 Hodenschläuche münden in einen Becher aus, der in die Mitte des Rückens liegt. Er verläuft, nur wenig verengt als Samenleiter dem Schwanz zu, so dass er nur als eine Erweiterung desselben zu betrachten ist." It should be explained that Zenker counted the blind section of the vas deferens as a fifth testicle. He showed (in his Pl. 5, fig. 1) the four testes and the



Figs. 1-7.—*Candona subvulvata* Hoff. 1-4. Selected cross sections of a male. Sections are 10-microns thick and stained with Ehrlich's haematoxylin and eosin. 1. Section through the oral region, showing the large seminal vesicles filled with spermatozoa. 2. Section through the front ends of the Zenker's organs, showing sections of the looped part of the vas deferens near the center; at the upper right, the spermatozoa in the seminal vesicle are entering the funnel-shaped adit of the Zenker's organ. 3-4. Sections through the middle of the Zenker's organs, showing several spermatozoa in the central tube of each. 5. Parasagittal section of a male, slightly inclined, stained with Ehrlich's haematoxylin and eosin. Parts of the four testes in this half of the

blind section of the vas deferens joined to an enlargement of the vas deferens, which continued as a narrower tube to the penis; in this illustration Zenker's organ was connected separately to the penis.

It was Stuhlmann (1886, p. 549) who first gave a good description of the seminal vesicle in Cyprididae, when he wrote:

Das Vas deferens mündet in das proximale Ende des Ejaculationsapparates ein. Bei Cypris ist diese Verbindung ziemlich leicht zu sehen, weil hier das Vas deferens sich oft stark erweitert und die Spermatozoen, welche wahrscheinlich nur einzeln den Ejaculationsapparat passiren können, sich hier, wie in einer Art von Samenblase anhäufen; man sieht dann deutlich, wie dieselben in einem dicken Bündel in den oberen Trichter des Ejaculationsapparates hineindringen.

Nevertheless, Stuhlmann's contribution was ignored and G. W. Müller figured (1889, Pl. 32, fig. 6; 1894, unnumbered text fig.) the wide part of the vas deferens as preceding both the blind section of the vas deferens and the Zenker's organ. His "birnförmige Erweiterung" was shown as a vesicle near the junction of the testes. Müller's 1894 figure was reproduced by Klie (1926, fig. 20). Other writers have not mentioned a wide section of the vas deferens.

In *Candonia suburbana* Hoff (fig. 1) the seminal vesicles are remarkably large. They are distended with spermatozoa and occupy one-eighth of the body. Their anterior ends reach nearly to the wall of the forehead (fig. 8). As shown in figs. 2 and 5, the posterior end of each seminal vesicle lies in the funnel-shaped indentation of the Zenker's organ. There is no narrow section of the vas deferens between the seminal vesicle and Zenker's organ in any of the 25 specimens of *Candonia* which I have examined in detail.

SPERMATOZOA IN ZENKER'S ORGANS

Writers disagree as to whether spermatozoa normally lie in Zenker's organ. Rehberg (1884, p. 15) said, "Der innere Cylinder ist, wie man es leicht beim Auseinanderziehen der Chitinkränze wahrnehmen kann, mit Spermatozoen angefüllt." Nordqvist, however, denied that spermatozoa enter the organ except during copulation. He wrote (1885, p. 162), ". . . der Apparat, wenn das Thier nicht in Kopulation begriffen ist, nie Spermatozoen enthält."

As can be seen in figs. 3-4, Zenker's organs contain spermatozoa. In six males of *Candonia suburbana* which were sectioned, each Zenker's organ had several spermatozoa within it. The animals were not in copulation when killed, so that spermatozoa in the organ seem to be the normal condition, at least within this species. It seems highly unlikely that in each specimen which was sectioned the spermatozoa could have been forced through the small opening and into Zenker's organ by the embedding and sectioning process.

Another question concerns the number of spermatozoa in Zenker's organ

animal can be seen in the hypodermis. The seminal vesicle, distended with spermatozoa, enters the front end of Zenker's organ, which is incomplete in this section. In Zenker's organ parts of five wreaths of chitin spines, the chitin rings of the central tube, and the muscles can be seen. 6-7.—*Candonia fossulensis* Hoff. Zenker's organs from Paratype TL25, collection of the late Dr. Harley J. Van Cleave, mounted in diaphane and stained with acid fuchsin (?). Each of these organs contains eight wreaths of chitin spines. The chitin rings around the central tube show up in these photographs.

(Figs. 1-5 to scale shown in fig. 5; figs. 6-7 to scale shown between them.)

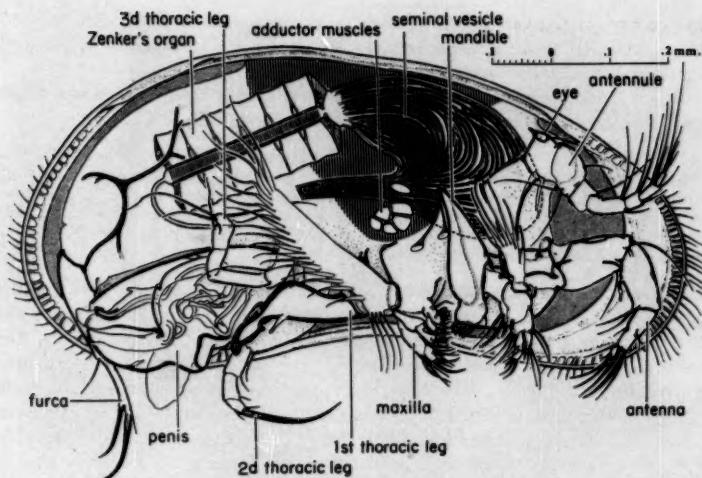


Fig. 8.—*Candona suburbana* Hoff. Male with right valve and part of the body wall removed to show the body, appendages, seminal vesicle, and Zenker's organ on the right side. The vertically hatched area represents the junction of the body wall and the hypodermis.

at one time. Weismann (1880) thought that the narrow anterior opening would admit only one spermatozoon at a time. Nordqvist (1885, p. 163) stated positively, ". . . nur ein Spermatozoon auf einmal in den Apparat eindringen kann." Schwarz (1888) believed that a major function of the organ was to isolate spermatozoa and allow them to pass one at a time.

Figs. 3-4 shows several spermatozoa within each organ. Whether they enter singly or not, I cannot say, but certainly more than one lies in the organ at one time.

NUMBER OF WREATHS IN CANDONA

There is no statement published that male ostracods of the genus *Candona* have more or fewer than seven wreaths of chitinous spines in each of the Zenker's organs. The number seven has been stated by Zenker (1850; 1854), Rehberg (1884), Vávra (1891), Klie (1926), and others. Sars (1923) considered seven wreaths in Zenker's organ to be a generic character of *Candona*. It is true that Klie (1938) said that the organ in the subfamily *Candocyprinae*, to which he assigned *Candona*, had six to eight wreaths, but he gave no number for the genus. Similarly, Hoff (1942, p. 53) stated that the subfamily *Candoninae* had males "usually with seven wreaths of chitinous spines," but gave no additional information for *Candona* or its species.

One specimen has come to my attention in which the Zenker's organs each have eight wreaths (figs. 6-7). It is a paratype of *Candona fossulensis* Hoff. Hoff deposited this type in the care of the late Dr. Harley J. Van Cleave,

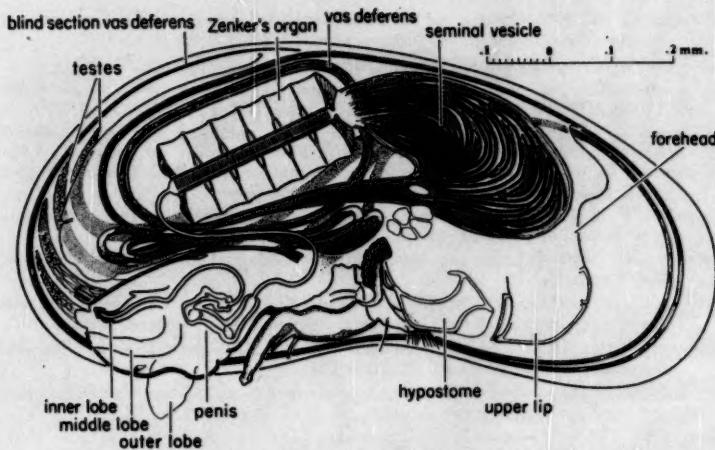


Fig. 9.—*Candonia suburbana* Hoff. Male cut along the median sagittal plane to show the sex system in the left half of the animal. The Zenker's organ is cut in half to show the central tube.

through whose courtesy I studied it in 1948. Although the supernumerary wreath in each of the organs must be regarded as an abnormality, its occurrence casts some doubt on the significance of the number of wreaths as a generic or subfamilial character.

Acknowledgments.—I am greatly indebted to the late Dr. Harley J. Van Cleave of the University of Illinois, under whose direction this study was started in 1948. His enthusiastic support and encouragement contributed much to the ideas presented above. Shortly before his death, Dr. Van Cleave offered valuable criticism of the preliminary draft of this paper.

I wish to express my thanks to Miss Marion Birkner, University of Illinois, who, in 1948, prepared the sections illustrated in the plate.

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Studies on Monogenetic Trematodes. XXI. North American Gyrodactylinae, Dactylogyrrinae and a New Host Record for *Urocleidus dispar* (Mueller, 1936)¹

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In 1922 Johnston and Tiegs established the Gyrodactyloidea as one of the two superfamilies of the suborder Monopisthocotylea Odhner, 1912. Subsequently, Bychowsky (1933a) established the family Dactylogyridae to include certain species previously placed in the genus *Gyrodactylus* (Gyrodactylidae). So much work has been done on the genus *Dactylogyrus* that by comparison, the genus *Gyrodactylus* appears somewhat neglected. Species of the latter genus, like those of *Dactylogyrus*, have been described from Europe, North America, continental Asia, and Japan.

As early as 1901, Atkins reported *Gyrodactylus elegans* v. Nordin. from fishes of Maine and later, Guberlet, Hansen, and Kavanaugh (1927) reported it from Washington but Price (1937) doubted the identity of this species and commented ". . . whether these reports indicate the occurrence of the European species by that name is open to question." This statement also applied to the North American report of Cooper (1915) for *G. medius* Katheriner. Cooper's illustration indicates the validity of Price's opinion since it does not represent *G. medius*. The first authentic report of a new species of *Gyrodactylus* in North America was by Van Cleave (1921), who described *G. fairporti* from *Cyprinus carpio* and *Ameiurus melas*. In 1932, Mueller and Van Cleave described *G. elegans* from *Carassius auratus* and described *G. spathulatus* from *Catostomus commersonii* taken near Bridgeport, New York. Other reliable reports are: *G. gurleyi* Price 1937, from a Japanese gold fish; *G. stegurus* Mueller, 1937, and *G. stephanus* Mueller, 1937, from *Fundulus diaphanus* and *F. heteroclitus*, respectively. In 1953, Hargis reported *G. elegans* from *Lepomis m. macrochirus* from Virginia and more recently (1955) he described *G. funduli* from *Fundulus similis* and *G. prolongis*² from *Fundulus grandis* and also recorded *G. stephanus* Mueller, 1937, from *Fundulus grandis* (all) from Florida. Unidentified species were reported by Stunkard and Dunihue (1933), Linton (1940),² and Hargis (1955). Ikezaki (1955) described *G. incisura* from *Eucalia inconstans* from North Dakota.³ The

¹ A portion of a thesis submitted by the senior author to the University of Notre Dame in partial fulfillment of the requirements of the degree of Doctor of Philosophy.

² *Gyrodactylus* sp. Linton, 1940, is now *G. prolongis* Hargis, 1955.

³ Unpublished dissertation, therefore *G. incisura* has no validity at present.

seven descriptions in the present work bring the total of *Gyrodactylus* species in North America to seventeen (one exotic and one unpublished).

Fifty species of *Dactylogyrus* were reported for North America by Monaco and Mizelle in 1955. These authors summarized the information for the genus and their paper should be consulted for pertinent information. Four new species of *Dactylogyrus* are described in the present investigation.

A comparative description of *Urocleidus dispar* (Mueller, 1936) Mizelle and Hughes, 1938, is presented from specimens taken from *Archoplites interruptus* (Girard), a new host for this parasite. For a review of this genus *Urocleidus* (*Tetraonchinae*) see Mizelle et al. 1956.

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MATERIALS AND METHODS

Fish hosts in the present investigation were collected from California, Indiana, Michigan, Nevada, Texas, and British Columbia. They were frozen as recommended by Mizelle (1938) and then preserved in 2.5% formalin. The gills were removed, placed in small vials, about $\frac{1}{2}$ to $\frac{2}{3}$ full of tap water, and shaken vigorously to free the worms from the branchial tissue. The material was then transferred to Syracuse watch glasses, and diluted and decanted until clear enough for reliable examination with a dissecting microscope.

Individual specimens were collected with a capillary pipette equipped with a rubber bulb and transferred, one each, to a depression in a drop of solidified glycerine-gelatin medium on a clean glass slide. A cover glass which was placed thereon settled in place as the medium was melted with gentle heat. The slide was allowed to cool, the mounting medium solidified, the edges of the cover glass were sealed with ringing varnish, and a permanent mount was thus produced. All available specimens up to a maximum of 20 were used in the description of each species.

Measurements were made with a compound microscope and a calibrated ocular micrometer for 1) body length, 2) greatest body width, 3) haptor width, 4) haptor length, 5) length of haptoral bars, 6) length of anchors, 7) width of anchors, 8) length of hooks,⁴ 9) length of cirrus, 10) length of accessory piece, and 11) transverse diameter of pharynx. Curved structures were measured as a straight line extending between the two most distant points of the structure. Measurement of anchor length, for example, extends from the tip of the longest root of the base to the most distant point on the curved portion in the region of junction of the shaft and point. The width of the anchor is the greatest width of an anchor base. Mean measurements were calculated for three or more specimens and each consists of an average of the measurements of the same structure in the different specimens. Maxima and minima are given in parentheses following a mean value. Measurements in

⁴ Length of hooks in the case of the *Gyrodactylus* species did not include the shaft because of 1) difficulty in measuring these along the curved margins of the haptor and 2) in many cases the ends of the shafts were hidden by anchors, cuticular plates and bars.

quotation marks are those from a comparative description by Mizelle and Cronin (1943) and are cited in a comparative manner in the description of *U. dispar* (Mueller, 1936), Mizelle and Hughes, 1938.

GENERAL MORPHOLOGY OF SPECIES OF *GYRODACTYLUS* AND *DACTYLOGYRUS*

Members of the genus *Gyrodactylus* are trematodes of small-to-fairly large size (ca. 0.22 mm-0.88 mm long) that parasitize the gills and skin of fishes and amphibians. The body is flattened dorsoventrally and consists of two tandem portions: a trunk or body proper and a posterior haptor or hold-fast organ. The trunk is divisible into a cephalic area (without eyespots) and a posterior part containing the 1) pharynx, 2) remaining parts of the digestive system posterior to this structure, 3) reproductive systems, etc. The cephalic region is bilobed and usually possesses one or two minute, boring spines. Papillae, one on each cephalic lobe, were referred to as "sensory papillae" by Mueller and Van Cleave (1932). This designation is considered incorrect since it is obvious that these papillae serve as outlets for secretions of some if not all of the cephalic glands by way of the contained head organs (see Lühe, 1909, fig. 6). The cephalic glands consist of two groups situated bilaterally at or near the level of the pharynx and empty through ducts to the head organs which consist of enlargements of the terminal portions of the ducts which may be supplemented with glandular tissue. The pharynx is invariably well developed and in many cases terminates anteriorly in a closely associated buccal cavity or buccal tube (prepharynx) which is nonmuscular. The esophagus bifurcates posterior to the pharynx to produce two intestinal crura that end blindly in the region of the ovary.

The cirrus is situated ventrally and composed of an orbiculate vesicle on which there occurs a cuticularized plate possessing one large central structure (usually hooklike) and a number of smaller structures "hooklets" situated nearby. The longitudinal striae, representing muscle bundles, which Yin and Sproston (1948) reported as arising from each of the spines comprising the genital corona were not observed in the present investigation. The single testis is an ovate structure situated posterior to the uterus in the posterior portion of the trunk. A vas deferens is not readily discernible but apparently exists as a tube between the testis and the cirrus as described by previous authors.

The ovary lies immediately anterior to the testis and often contains a single egg. When an egg is lacking, many large nuclei are present, however this condition has been observed most often in the ovary of a fully developed embryo. The vitelline glands are unique in that they are confined to the posterolateral region of the trunk as a compact globular mass, extending as far forward as the level of the testis in relaxed specimens. These glands contain many fine granules, and are considered true vitellaria and not an ovary as interpreted by many authors.

The pretesticular ovary is closely associated with the uterus and is located axially in the midportion of the trunk. In almost all species treated herein, the uterus contained one or two embryos of different ages. The older embryo is invariably located in the posterior portion of the uterus with its haptor

directed posteriorly. The younger embryo when present, is oriented in the opposite manner. The opening of the uterus was not observed and the authors agree with Yamaguti (1940) that it is recognizable only during the birth of the embryo.

The posterior part of the trunk narrows to form a peduncle which attaches to, and is usually separated by a constriction from, the haptor. The haptor is circular or oval in outline (dorsal view) with a concave ventral surface. Ventrally it bears two large central hooks (anchors) whose bases are connected by one or two transverse bars, and sixteen small hooks arranged radially with their points directed outwardly.

The lack of consistency in the use of terminology for the structures of the gyrodactylid haptor necessitates a proposal for standardization. Mueller (1936) proposed the accepted term "anchors" for the large hooks and that of "hooks" for small hooks. Although authors previous to 1936 referred to anchors as "hooks" and to the hooks as "hooklets," Yamaguti (1940) reintroduced these obsolete terms which should be discarded. Such terms as "transverse clamps," "distal clamps" (Stunkard and Dunihue 1933); "dorsal" and "ventral" bars (Mueller 1936); "rudimentary crosspiece" (Mueller & Van Cleave 1932) are confusing and also should be discarded. "Superficial" and "deep" are hereby proposed for designating the bars on the superficial and deep surfaces of the anchors to replace the above terminology for these structures. These designations are consistent with those (superficial, deep) for the anchor roots as proposed by Mizelle (1938) to replace the terms "inner" and "outer" of Mueller (1936). The terms "dorsal" and "ventral" should be reserved for designation of the bars associated with the dorsal and ventral anchors in the tetraonchinae, etc.

Species of *Dactylogyrus* are remarkably similar to those of *Gyrodactylus* except for the following: 1) the cephalic area is not always bilobed, 2) four eyespots are present immediately anterior to the pharynx, 3) a conspicuous copulatory complex consisting of a cirrus and accessory piece is present instead of a vesicle supporting a cuticularized plate, 4) a lateral (usually) vagina is present, 5) the species are oviparous, 6) the haptoral hooks number 14 and are distributed on both sides of the haptor, 7) a vestigial ventral bar is present in some species and indicates the probable evolution of these forms from Tetraonchinae which possess a ventral as well as a dorsal pair of anchors, and 8) they occur exclusively on the gills of fishes.

Gyrodactylus bairdi n. sp.

Host and locality.—*Cottus b. bairdii* Girard, Judy Creek, Clay Twp., St. Joseph Co., Indiana.

Specimens studied.—Eleven.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55263, Wash., D. C.

Description.—Moderate sized gyrodactylid provided with a smooth thin cuticle, length 0.368 mm (0.296-0.404 mm), greatest width 0.072 mm (0.036-0.108 mm) usually in anterior half of trunk. Cephalic region bilobed, each lobe containing 1 or 2 head organs, ducts from cephalic glands to head organs conspicuous. Cephalic glands located postero-lateral to pharynx. Pharynx relatively large, highly muscular and circular in outline (dorsal view), posterior portion more muscular than lower buccal tube, transverse diameter 0.034 mm (0.029-0.038 mm). Peduncle short and tapered posteriorly. Haptor longer

than broad, concave ventrally and umbelloid in shape, width 0.067 mm (0.059-0.084 mm), length 0.076 mm (0.067-0.084 mm). Each anchor composed of 1) a base with a well-defined superficial root and a rudimentary deep root, 2) a hollow shaft, and 3) a hollow recurved point (Pl. 1, fig. 4). Anchor length 0.068 mm (0.065-0.070 mm), width of base 0.012 mm (0.011-0.013 mm). Superficial bar well developed, and with a conspicuous terminal structure at each end. An apron-like, conspicuously striated plate arises from posterior margin of this bar and extends between the anchor shafts (Pl. 1, fig. 3). Superficial bar length 0.024 mm (0.020-0.026 mm). Deep bar elongate with tapered ends and usually a medial constriction (Pl. 1, figs. 5-7), length 0.016 mm (0.014-0.018 mm). Hooks, sixteen in number, similar in shape, and arranged radially around the haptor with points emerging from ventral periphery. Each hook consists of 1) an elongate shaft, 2) a tapered base and 3) a recurved point (Pl. 1, fig. 2), hook length 0.008 mm. Vitellaria post-testicular and composed of a compact, anteriorly concave mass; individual vitelline follicles globose and conspicuous. Ovary immediately posterior to uterus, circular in outline (dorsal view) and usually contains a single egg. Testis elliptical in outline (dorsal view) and postovarian. Uterus located in midportion of trunk and conspicuous by the presence of one, or two embryos of different ages. Cirrus situated ventrally, immediately posterior to pharynx and slightly on left of body axis, spherical in shape and possesses a cuticularized plate and a number of hooklets (Pl. 1, fig. 1); cirrus diameter 0.009 mm (0.008-0.011 mm).

The closest apparent relative of *G. bairdi* is *G. micropogonius* n. sp. The superficial bar in these species is somewhat similar in shape (Pl. 1, figs. 3, 27), but that of *G. bairdi* does not possess the anteriorly directed lateral arms which are characteristic of *G. micropogonius*. The remaining haptoral structures in these two species are conspicuously different.

Gyrodactylus couesi n. sp.

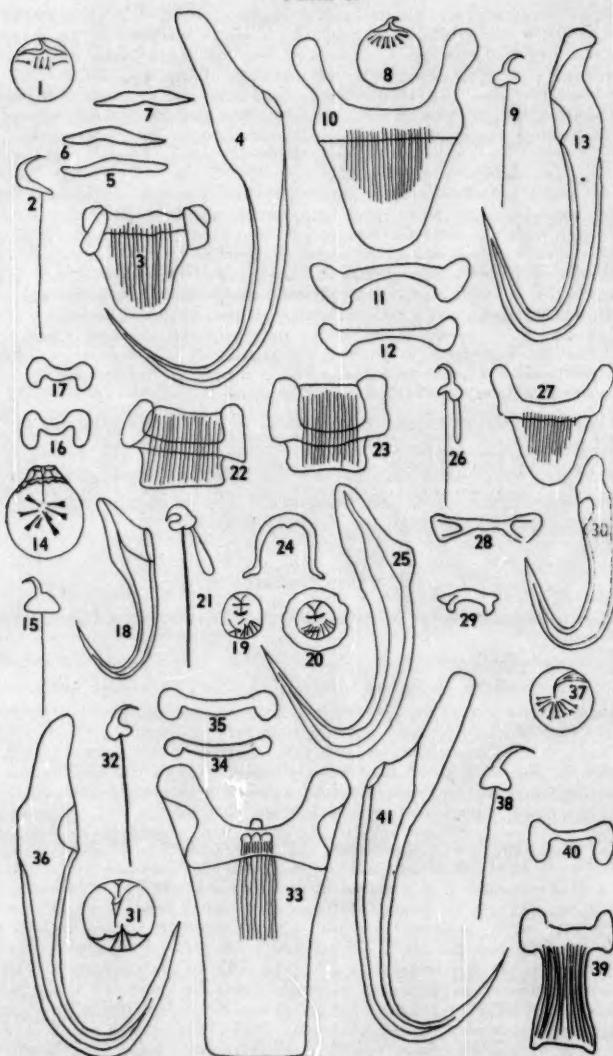
Host and locality.—*Couesi* *plumbi* *dissimilis* (Girard), Loon Lake, British Columbia, Canada.

Specimens studied.—Twelve.

Type specimens.—Type, U. S. N. M. Helm, Coll. No. 55264, Wash., D. C.

Description.—Relatively stout gyrodactylid, provided with a smooth, thin cuticle, length 0.314 mm (0.242-0.386 mm), greatest trunk width 0.090 mm (0.072-0.106 mm). Cephalic region bilobed, one papilla on each lobe. Cephalic glands situated bilaterally in cephalic area at level of pharynx; ducts between cephalic glands and head organs indistinct; head organs present in cephalic lobes. Pharynx transversely ovate-to-elliptical in outline (dorsal view), transverse diameter 0.034 mm (0.029-0.038 mm). Peduncle short and tapered posteriorly. Haptor circular in outline and umbelloid in shape, width 0.067 mm (0.042-0.088 mm), length 0.080 mm (0.072-0.097 mm). Anchors large and composed of 1) a base with a well-developed superficial root possessing medially directed end, and a deep root reduced to a vestige, 2) a hollow shaft, and 3) a hollow recurved point (Pl. 1, fig. 13); anchor length 0.061 mm (0.058-0.065 mm), width of base 0.011 mm (0.009-0.012 mm). Superficial root with a small projection directed medially which secures the superficial bar. Superficial bar possesses a relatively large posteriorly thickened striated plate and anteriorly rounded ends (Pl. 1, fig. 10), length 0.035 mm (0.031-0.047 mm). Deep bar variable, and terminates bilaterally in rounded knobs (Pl. 1, figs. 11, 12), length 0.026 mm (0.024-0.033 mm). Hooks, sixteen in number, similar in shape, and radially arranged on ventral surface of haptor. Each hook consists of 1) a slender elongate shaft, 2) a bilobed base, and 3) a mildly recurved point; hook length 0.031 mm (0.029-0.033 mm) (Pl. 1, fig. 9). Vitelline gland extensive, subspherical-to-globular, and situated posterior to testis. Ovary circular-to-ovate in outline (dorsal view), and located directly behind uterus; testis elliptical in outline (dorsal view) and situated posterior to ovary. Uterus prominent, situated in midportion of trunk and usually containing embryos in different stages of development. Cirrus ventral, posterior to pharynx, circular in outline and possessing a cuticularized plate composed of a recurved hook and 8 hooklets (Pl. 1, fig. 8).

PLATE 1.



Figs. 1-41.—*Gyrodactylus bairdi* n. sp. 1. Cirrus; 2. Hook; 3. Superficial bar; 4. Anchor; 5-7. Deep bar. *G. coesi* n. sp. 8. Cirrus; 9. Hook; 10. Superficial bar; 11, 12. Deep bar; 13. Anchor. *G. egregius* n. sp. 14. Cirrus; 15. Hook; 16, 17. Deep bar; 18. Anchor. *G. limi* n. sp. 19, 20. Cirrus; 21. Hook; 22, 23. Superficial bar; 24. Deep bar; 25. Anchor. *G. micropogonius* n. sp. 26. Hook; 27. Superficial bar; 28, 29. Deep bar; 30. Anchor. *G. rhinichthius* n. sp. 31. Cirrus; 32. Hook; 33. Superficial bar; 34, 35. Deep bar; 36. Anchor. *G. richardsonius* n. sp. 37. Cirrus; 38. Hook; 39. Superficial bar; 40. Deep bar; 41. Anchor.

The closest relative of *G. couesi* is *G. stephanus* Mueller, 1937. The superficial root of each anchor base is bent medially in these two species (Pl. 1, fig. 13; Mueller 1937, fig. 21M) and although the superficial bars are similar in shape (Pl. 1, fig. 10; Mueller 1937, fig. 24M) the hooks and deep bars are decidedly different (Pl. 1, figs. 9, 11, 12; Mueller 1937, 21M, 25M).

Gyrodactylus egregius n. sp.

Host and locality.—*Richardsonius egregius* (Girard). Lahotan Reservoir, Reno, Nevada.

Specimens studied.—Thirteen.

Type specimens.—Type, U. S. N. M. Helm. Coll. 55280, Wash., D. C.

Description.—Relatively small gyrodactylid provided with a smooth, thin cuticle, length 0.296 mm (0.242-0.368 mm), greatest width 0.116 mm (0.090-0.152 mm) usually present near midlength of trunk. Cephalic region bilobed; each lobe contains 3 to 5 head organs and an anterior indentation which produces a papilla or pseudopapilla. Cephalic glands located bilaterally near level of pharynx; ducts from cephalic glands to head organs indistinct. Pharynx transversely elliptical in outline (dorsal view) transverse diameter 0.046 mm (0.042-0.063 mm). Peduncle extremely short and constricted. Haptor concave ventrally, and umbelloid in shape; width 0.072 mm (0.046-0.084 mm), length 0.059 mm (0.046-0.076 mm). Each anchor composed of 1) a base with a well-developed superficial root and a deep root indicated by a slight indentation, 2) a hollow shaft, and 3) a hollow recurved point (Pl. 1, fig. 18). Anchor length 0.033 mm (0.031-0.037 mm), width of base 0.009 mm (0.008-0.011 mm). Superficial bar absent. Deep bar well developed and yoke shaped (Pl. 1, figs. 16, 17), length 0.009 mm (0.007-0.014 mm). Hooks, sixteen in number, similar in shape, and arranged in a radial manner with points emerging from the ventral periphery of the haptor. Each hook composed of 1) an elongate slender shaft, 2) a subtriangular base, and 3) a terminal recurved point (Pl. 1, fig. 15). Hook length 0.007 mm. Vitelline gland a compact mass circular-to-ovate in outline (dorsal view) and located in posterior portion of trunk near peduncle. Ovary elliptical in outline (dorsal view), located immediately posterior to uterus and usually contains a single egg. Testis elliptical in outline (dorsal view) and postovarian. Uterus present axially near midlength of trunk, usually contains one, or two embryos of different ages. Cirrus spherical, situated ventrally immediately posterior to pharynx and on left of body axis; cuticularized portion consists of a plate with a large single hook and 8 hooklets (Pl. 1, fig. 14); cirrus diameter 0.011 mm (0.009-0.019 mm).

The closest apparent relatives of *G. egregius* are *G. cylindriformis* Mueller and Van Cleave, 1932, and *G. fairporti* Van Cleave, 1921. These three species are unique in that they do not possess a superficial bar. The deep bar is conspicuously different in these three forms (Pl. 1, figs. 16, 17; Van Cleave 1921, fig. 1; Mueller and Van Cleave 1932, Pl. 17, fig. 10).

Gyrodactylus limi n. sp.

Host and locality.—*Umbra limi* (Kirtland), Judy Creek, Clay Twp., St. Joseph Co., Indiana.

Specimens studied.—Twelve.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55265, Wash., D. C.

Description.—Relatively large, elongate gyrodactylid provided with a smooth, thin cuticle, length 0.612 mm (0.580-0.882 mm), greatest width 0.116 mm (0.090-0.170 mm) generally present near midlength of trunk. Cephalic region with two inconspicuous lobes, a single papilla on each lobe. Cephalic glands (8, 9) immediately postero-lateral to pharynx, ducts from cephalic glands to head organs not observed, head organs present in each cephalic lobe. Pharynx subcircular in outline (dorsal view), transverse diameter 0.046 mm (0.042-0.055 mm). Peduncle short and tapered posteriorly. Haptor concave ventrally and umbelloid in shape, width 0.076 mm (0.059-0.110 mm), length 0.076 mm

(0.051-0.084 mm). Each anchor composed of 1) a base with a well-developed superficial root and a rudimentary deep root, 2) a hollow shaft, and 3) a hollow point (Pl. 1, fig. 25). Anchor length 0.068 mm (0.051-0.074 mm), width of base 0.016 mm (0.011-0.024 mm). Superficial bar broadly U-shaped and with a squarish plate extending from near anterior limits of bar posteriorly between anchor shafts (Pl. 1, figs. 22, 23), length 0.016 mm (0.012-0.022 mm). Deep bar horseshoe shaped with small lateral extensions at each end (Pl. 1, fig. 24), length 0.022 mm (0.018-0.026 mm). Hooks sixteen in number, similar in shape, and arranged radially around the haptor; points emerge from the ventral periphery. Each hook consists of 1) an elongate shaft, 2) a relatively massive base, and 3) a heavy recurved point (Pl. 1, fig. 21). A posteriorly projecting process arises from the base of each hook; hook length 0.037 mm (0.028-0.045 mm). Vitelline gland a compact mass circular-to-ovate in outline (dorsal view) and located in posterior portion of trunk near peduncle. Trunk parenchyma contains many fine scattered melanistic granules, which form two lateral bands in region of the uterus when distended with embryos. Ovary oval in outline (dorsal view) and pretesticular; testis elliptical in outline (dorsal view). Uterus containing one or two embryos (different ages), situated in midportion of trunk. Cirrus subspherical-to-spherical, situated ventrally immediately behind pharynx on left of body axis, and possesses a cuticularized plate as shown in Pl. 1, figs. 19, 20; greatest diameter of cirrus 0.012 mm (0.010-0.018 mm).

The unique horseshoe shaped deep bar of *G. limi* (Pl. 1, fig. 24) is different from that of any other member of the genus. *G. cylindriformis*, also a parasite of *Umbra limi*, shows no close morphological relationship with *G. limi* n. sp.

Gyrodactylus micropogonus n. sp.

Host and locality.—*Micropogon undulatus* (Linnaeus), South Jetty, Aransas Pass, Corpus Christi, Texas.

Specimens studied.—Three.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55266, Wash., D. C.

Description.—Relatively small gyrodactylid provided with a smooth, thin cuticle, length 0.296 mm (0.260-0.350 mm) greatest width 0.108 mm (0.090-0.116 mm usually present near midlength of trunk). Cephalic region bilobed, each lobe bearing a papilla possessing a group of 2 or 3 minute cuticular spines; head organs observed with difficulty, two to each lobe; cephalic glands anterolateral to, and on each side of, pharynx; ducts from cephalic glands to head organs not observed. Pharynx subspherical in outline (dorsal view), transverse diameter 0.034 mm. Peduncle short and tapered posteriorly. Haptor subspherical-to-transversely-ovate in outline (dorsal view), width 0.057 mm (0.055-0.059 mm), length 0.051 mm (0.046-0.055 mm). Each anchor consists of 1) a base with a well-developed superficial root and a rudimentary deep root, 2) a hollow shaft, and 3) a hollow recurved point (Pl. 1, fig. 30). A medially directed process on each superficial root facilitates securing the superficial bar. Anchor length 0.038 mm (0.037-0.039 mm), width of base 0.007 mm (0.006-0.008 mm). Superficial bar with anteriorly directed ends and a striated plate on the posterior border (Pl. 1, fig. 27), length 0.016 mm (0.014-0.018 mm). Deep bar elongate and quite variable (Pl. 1, figs. 28, 29), length 0.020 mm. Hooks, sixteen in number, similar in shape, and arranged in a radial manner in the haptor with points emerging from the ventral periphery. Each hook consists of 1) an elongate shaft, 2) a bilobed base, and 3) a sickle-shaped termination (Pl. 1, fig. 26). A bag-like process arises on the base of each hook. This structure extends posteriorly for about one-half the length of hook shaft. Hook length 0.006 mm. Vitelline gland globular and situated in the posterolateral region of trunk. Ovary elliptical in outline (dorsal view) and located immediately behind uterus; testis not observed. Uterus situated in midportion of body and contains one, or two embryos of different ages. Cirrus circular in outline (dorsal view), located dorsally and immediately behind pharynx on left of body axis. Details of cirrus were insufficiently distinct for purposes of illustration; cirrus diameter 0.010 mm.

The closest apparent relative to *G. micropogonus* is *G. coesi* n. sp. Whereas the superficial bars in these species are somewhat similar (Pl. 1, figs.

10, 27), the remaining haptoral structures are dissimilar (Pl. 1, figs. 9, 11-13, 26, 28-30).

Gyrodactylus rhinichthius n. sp.

Host and locality.—*Rhinichthys osculus robustus* (Rutter), Lahotan Reservoir, Reno, Nevada.

Specimens studied.—Twenty.

Type specimens.—Type U. S. N. M. Helm. Coll. No. 55267, Wash., D. C.

Description.—Relatively small gyrodactylid provided with a smooth, thin cuticle, length 0.260 mm (0.224-0.350 mm), greatest width 0.090 mm (0.072-0.116 mm), usually present in the posterior portion of the trunk. Cephalic region bilobed and with a papilla on each lobe. One pair of head organs observed in each lobe; cephalic glands present bilaterally at level of anterior portion of pharynx; ducts from head organs to cephalic glands not observed. Pharynx transversely elliptical-to-subspherical in outline (dorsal view), transverse diameter 0.029 mm (0.025-0.033 mm). Peduncle short and stout. Haptor umbrellloid and invariably overlaps posterior portion of trunk, width 0.055 mm (0.046-0.084 mm), length 0.067 mm (0.059-0.097 mm). Anchors comparatively large, each composed of 1) a base with a moderately developed superficial root and a rudimentary deep root, 2) a long slender hollow shaft, and 3) a hollow recurved point (Pl. 1, fig. 36), length 0.057 mm (0.053-0.066 mm), width 0.010 mm (0.009-0.011 mm). Superficial root of each anchor possesses a medially directed process which secures the superficial bar. Superficial bar moderately wide with anteriorly directed arms and provided with an elongate, truncate, cuticular plate which possesses medial striations (Pl. 1, fig. 33). Superficial plate extends to proximal portion of anchor points; superficial bar length 0.033 mm (0.028-0.037 mm). Deep bar narrow and terminates bilaterally in knob-like structures (Pl. 1, figs. 34, 35). Deep bar length 0.024 mm (0.020-0.026 mm). Hooks, sixteen in number, similar in shape, and radially arranged in the haptor with points emerging from ventral periphery. Each hook consists of 1) a long slender shaft, 2) a bilobed base, and 3) a sickle-shaped termination (Pl. 1, fig. 32), hook length 0.008 mm. Vitelline gland a conspicuous compact mass, circular-to-oval in outline (dorsal view), highly refractile and located in posterior portion of trunk. Ovary subspherical in outline (dorsal view), located immediately posterior to uterus and often containing a single egg. Testis spherical-to-ovoid and situated posterior to ovary. Uterus located in midportion of trunk and containing one, or two embryos of different ages. Cirrus spherical, situated dorsally immediately behind pharynx on left of body axis and possessing a cuticular plate with structures as shown in Pl. 1, fig. 31.

G. rhinichthius has no apparent close relative. *G. spathulatus* has anchors (Mueller 1936, Pl. 12, fig. 1) which remotely resemble those of the present species (Pl. 1, fig. 36), but there is no similarity between the haptoral bars of these two species (Pl. 1, figs. 33-35; Mueller 1936, Pl. 12, fig. 1).

Gyrodactylus richardsonius n. sp.

Host and locality.—*Richardsonius egregius* (Girard), Lahotan Reservoir, Reno, Nevada.

Specimens studied.—Two.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55268, Wash., D. C.

Description.—Relatively small gyrodactylid provided with a smooth thin cuticle, length 0.224-0.386 mm, greatest width 0.090-0.108 mm, usually present near midlength of trunk. Cephalic region bilobed with a papilla on each lobe; head organs indistinct. Cephalic glands situated bilaterally at level of pharynx; ducts from cephalic glands to head organs not observed. Pharynx highly muscular and transversely elliptical (dorsal view), transverse diameter 0.034-0.042 mm. Peduncle short and tapered posteriorly. Haptor umbrellloid, concave ventrally, width 0.073-0.076 mm, length 0.067-0.080 mm. Anchors large, each consists of 1) a base with a well-developed superficial root and a rudimentary deep root, 2) a hollow tapered shaft, and 3) a hollow recurved point (Pl. 1, fig. 41). Anchor

length 0.070-0.072 mm, width of base 0.011-0.018 mm. Superficial bar modified into a flat, finely striated plate which terminates posteriorly between and about midway the anchor shafts, length 0.018 mm (Pl. 1, fig. 39). Deep bar narrowly elongate, straight or slightly bent in midportion with each end rounded into a posteriorly directed process (Pl. 1, fig. 40), length 0.024 mm. Hooks, sixteen in number, similar in shape, radially arranged and with points emerging from the haptoral margin. Each hook consists of 1) a shaft, 2) a relatively large base, and 3) a sickle-shaped termination; hook length 0.009 mm. Vitelline gland obscured by anterior margin of haptor. Ovary elliptical in outline (dorsal view), located immediately behind uterus; testis not observed. Uterus located near midlength of trunk and usually contains one embryo. Cirrus spherical, located ventrally immediately posterior to the pharynx and on left of body axis. Cuticular plate of cirrus possesses one large hook and eight small hooklets arranged in semicircular fashion in front of the former; cirrus diameter 0.014 mm (Pl. 1, fig. 37).

The closest relative of *G. richardsonius* is *G. atherinæ* Bychowsky, 1933b. The anchors of these forms are similar but differ in shape of the superficial roots and the presence of membranous bags on the anchor points of *G. atherinæ*.

Dactylogyrus nuchalis n. sp.

Host and locality.—*Hybognathus* n. *nuchalis* Agassiz, Sulphur River, Texarkana, Texas.

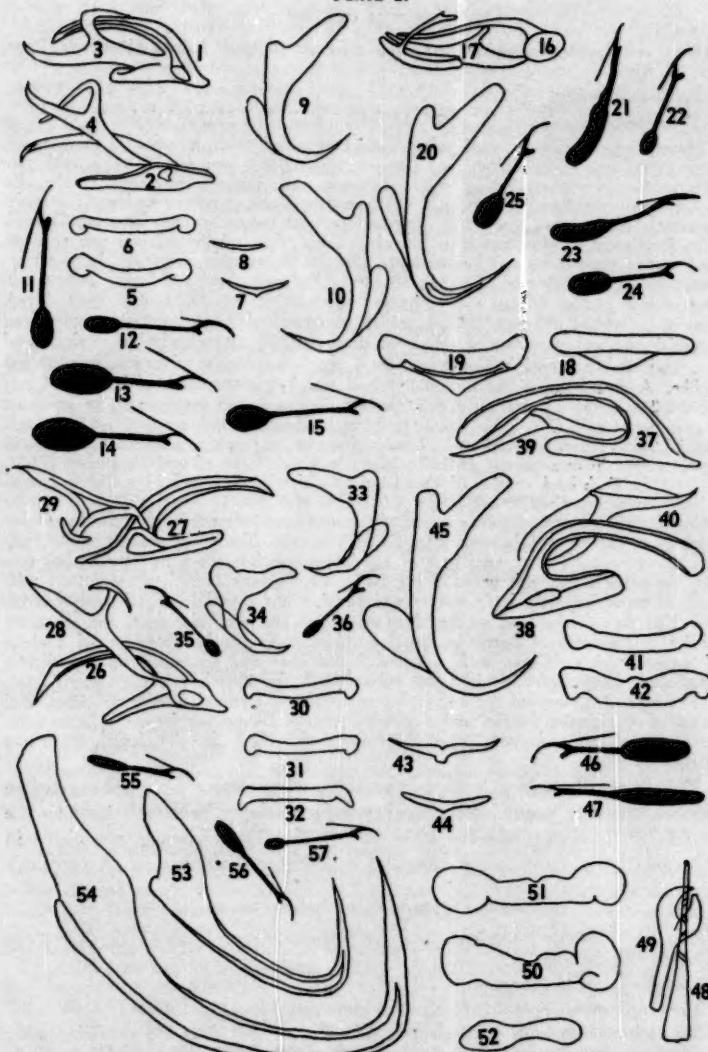
Specimens studied.—Twenty.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55269, Wash., D. C.

Description.—Relatively small dactylogyrid provided with a smooth thin cuticle, length 0.206 mm (0.152-0.260 mm), greatest width 0.054 mm (0.036-0.072 mm) usually present in posterior half of trunk. Eyespots four, approximately equal in size, distance between members of each pair approximately equal; accessory melanistic granules infrequently present in cephalic area. Cephalic lobes and head organs inconspicuous. Pharynx observed with difficulty, subspherical in outline (dorsal view), transverse diameter 0.017 mm (0.013-0.025 mm). Peduncle short, haptor broader than long, greatest width of haptor 0.034 mm (0.021-0.042 mm), length 0.029 mm (0.021-0.046 mm). Each anchor composed of 1) a base with well-defined superficial and deep roots (former much longer), 2) a slender shaft, and 3) a mildly recurved hollow point (Pl. 2, figs. 9, 10). Anchor wings conspicuous, membranous and bag-like. Anchor length 0.028 mm (0.024-0.029 mm), greatest width of base 0.011 mm (0.009-0.016 mm). Dorsal bar slightly bent posteriorly in midportion and with knob-like ends (Pl. 2, figs. 5, 6), dorsal bar length 0.012 mm (0.011-0.014 mm). Vestigial ventral bar (often not visible) usually bent posteriorly in midportion and with slender tapering ends (Pl. 2, figs. 7, 8); length 0.012 mm (0.011-0.022 mm). Hooks, fourteen in number and normal in arrangement (Mizelle 1938). Each hook consists of 1) an elongate oval base, 2) a slender solid shaft, and 3) a sickle-shaped termination with an opposable piece (Pl. 2, figs. 11-15). Bases of members of pairs nos. 1 and 5 usually smaller than those in other hooks. Posteriorly projecting process on sickle-shaped termination short and well differentiated. Hook length 0.016 mm (0.014-0.018 mm). Vitellaria highly developed and extend from posterior level of pharynx to anterior portion of peduncle. Gonads obscured by dense vitellaria. Two prostates of approximately equal size situated laterally near cirrus base, both filled with granular material. Vagina present on right body margin in posterior part of anterior half of trunk, seminal receptacle conspicuous and in close proximity to vagina. Egg pore situated ventrally in rear of vestibular pore of copulatory complex. Copulatory complex consists of a cirrus and accessory piece. Cirrus with a relatively narrow base and a long, thin, tapering shaft terminating in a fine point (Pl. 2, figs. 1, 3). Cirrus length 0.031 mm (0.029-0.037). Accessory piece attached basally to cirrus and consists of a shaft and a mildly recurved point; a lateral projection arises near midlength of the shaft and extends over cirrus shaft (Pl. 2, figs. 3, 4), length 0.026 mm (0.021-0.029 mm).

Copulatory complex superficially resembles that of *D. banghami* Mizelle and Donahue, 1944. However the extension of the lateral projection of the accessory piece is not present on the latter species and further the haptoral armament of the two species is dissimilar.

PLATE 2.



Figs. 1-57.—*Dactylogyrus nuchalis* n. sp. 1, 2. Cirrus; 3, 4. Accessory piece; 5, 6. Dorsal bar; 7, 8. Vestigial ventral bar; 9, 10. Anchor; 11-15. Hooks. *D. osculus* n. sp. 16. Cirrus; 17, Accessory piece; 18, 19. Dorsal bar; 20. Anchor; 21-25. Hooks. *D. rhinichthius* n. sp. 26, 27. Cirrus; 28, 29. Accessory piece; 30-32. Dorsal bar; 33, 34. Anchor; 35, 36. Hooks. *D. semotilus* n. sp. 37, 38. Cirrus; 39, 40. Accessory piece; 41, 42. Dorsal bar; 43, 44. Vestigial ventral bar; 45. Anchor; 46, 47. Hooks. *Urocleidus dispar* (Mueller, 1936) 48. Cirrus; 49. Accessory piece; 50, 51. Dorsal bar; 52. Ventral Bar; 53, Ventral anchor; 54, Dorsal anchor; 55-57. Hooks.

Dactylogyrus osculus n. sp.

Host and locality.—*Rhinichthys osculus robustus* (Rutter) Lahotan Reservoir, Reno, Nevada.

Specimens studied.—Ten.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55270, Wash., D. C.

Description.—Relatively small dactylogyrid provided with a smooth, thin cuticle, length 0.206 mm (0.188-0.260 mm), greatest width 0.090 mm (0.072-0.116 mm) generally present in anterior half of trunk. Eyespots four, approximately equal in size, distance between members of each pair approximately equal, accessory melanistic granules (apparently of the same type which comprise eyespots) present in cephalic area. Cephalic region incipiently divided medially, individual lobes often subdivided into two portions. Head organs present but not conspicuous. Pharynx transversely elliptical (dorsal view), greatest diameter 0.029 mm (0.025-0.038 mm). Peduncle short and broad; haptor sub-rectangular in outline (dorsal view), greatest width 0.046 mm (0.042-0.55 mm), length 0.046 mm (0.038-0.055 mm). Each anchor composed of 1) a base with well-defined superficial root and a moderately developed deep root, 2) a terminally hollow shaft, and 3) a moderately recurved hollow point (Pl. 2, fig. 20). Anchor wings membranous and bag-like. Anchor length 0.037 mm (0.035-0.041 mm), greatest width of base 0.014 mm (0.012-0.016 mm). Dorsal bar slightly variable in shape, and usually with an apron on the posterior margin (Pl. 2, figs. 18, 19); dorsal bar length 0.024 mm (0.022-0.026 mm). Vestigial ventral bar, not observed. Hooks, fourteen in number approximately equal in length, normal in arrangement (Mizelle 1938) and with bases of variable shapes (Pl. 2, figs. 21-25). Each hook consists of 1) a base, 2) a slender shaft and 3) a slightly curved sickle-shaped termination. Hook length 0.020 mm (0.018-0.022 mm). Vitellaria heavily developed and extending from region of pharynx to anterior portion of peduncle. Ovary conspicuous, globose and located near middle of trunk. Testis obscured by dense vitellaria; two prostates present near base of copulatory complex, one with clear hyaline contents, the other filled with granular material. Vagina cuticularized, situated near mid-length of trunk, on right body margin and empties into a well-developed seminal receptacle. Egg pore ventral and situated between vagina and vestibular pore, and characterized by the presence of numerous papillae. Copulatory complex composed of a cirrus and accessory piece. Cirrus with a funnel-shaped base and a slender, hollow, slightly curved shaft which terminates in a fine point (Pl. 2, fig. 16); length 0.028 mm (0.020-0.031 mm). Accessory piece of complex morphology, attached basally to cirrus, and consists of a tripartite portion and a parallel process. A process from the latter arises near the distal end and passes across the cirrus shaft (Pl. 2, fig. 17), length 0.018 mm (0.016-0.024 mm).

This species is unique in that it possesses an accessory piece not heretofore described for this genus. Its closest apparent relative with reference to the cirrus is *D. confusus* Mueller 1938 (Pl. 4, fig. 1). However, the cirrus in *D. osculus* has a much larger base and a slenderer shaft than in *D. confusus*.

Dactylogyrus rhinichthius n. sp.

Host and locality.—*Rhinichthys atratulus meleagris* Agassiz, Judy Creek, Clay Twp., St. Joseph Co., Indiana.

Specimens studied.—Twenty.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55271, Wash., D. C.

Description.—Relatively small dactylogyrid provided with a cuticle exhibiting many fine transverse striations encircling the trunk from level of pharynx to, and infrequently part of, the haptor. Body length 0.170 mm (0.152-0.206 mm), greatest width 0.072 mm (0.054-0.090 mm) usually present near midlength of trunk. Eyespots four, approximately of equal size, members of posterior pair somewhat larger and approximately the same distance apart as those of the anterior pair. Accessory melanistic granules observed infrequently in region of cirrus and vagina. Cephalic region conspicuously divided by a median groove and each lateral half being subdivided into two lobes. Three or four head organs present in each lobe; cephalic glands located posterolateral to head organs. Pharynx

subpherical-to-transversely ovate in outline (dorsal view), transverse diameter 0.055 mm (0.046-0.059 mm). Peduncle short and stout. Haptor broader than long, width 0.055 mm (0.048-0.076 mm), length 0.038 mm (0.034-0.046 mm). Each anchor composed of 1) a base with a well-defined superficial root extending almost at right angles to anchor shaft, and a rudimentary deep root, 2) a solid shaft, and 3) a solid point (Pl. 2, 33, 34); length 0.016 mm (0.014-0.022 mm), greatest width of base 0.012 mm (0.006-0.018 mm). Anchor wings membranous and distinctly bag-like. Dorsal bar narrowly elongate with rounded-to-truncate ends, midportion bent posteriorly, length 0.018 mm (0.016-0.022 mm) (Pl. 2, figs. 30-32). Ventral bar not observed. Hooks fourteen in number, normal in arrangement (Mizelle 1938) and approximately equal in size. Each hook consists of 1) a short oval base, 2) a long slender shaft, and 3) a sickle-shaped termination with an opposable piece; posteriorly projecting process conspicuous (Pl. 2, figs. 35, 36). Hook length 0.014 mm (0.012-0.016 mm). Vitellaria poorly developed and extend from the posterior level of pharynx to anterior portion of peduncle. Gonads occasionally observed, both ovate in shape, ovary pretesticular. Two prominent botuliform prostates present, usually displaced to left of median axis near cirrus base and both containing granular material. Vagina lightly cuticularized and located on right trunk margin near midlength. Seminal receptacle of moderate size and present near vagina. Copulatory complex consists of a cirrus and accessory piece. Cirrus a slightly curved tube with a truncate termination (Pl. 2, figs. 26, 27); length 0.033 mm (0.028-0.041 mm). Accessory piece attached basally to cirrus, slightly bent in midportion and with a slightly recurved tip; a lateral recurved process present on medial portion of shaft passes over and around cirrus and terminates in a crescentic process (Pl. 2, figs. 28, 29); length 0.028 mm (0.024-0.031 mm).

This species is distinguishable from all other members of this genus by the presence of cuticularized transverse striations on the trunk. The anchors of *D. rhinichthius* (Pl. 2, figs. 33, 34) are similar to those of *D. amblops* Mueller 1938 (Pl. 3, fig. 28), however the superficial root in the latter is not as long and slender as that of *D. rhinichthius*.

Dactylogyrus semotilus n. sp.

Host and locality.—*Semotilus a. atramaculatus* (Mitchill), Pickeral Lake Outlet, Cass Co., Michigan.

Specimens studied.—Nine.

Type specimens.—Type, U. S. N. M. Helm. Coll. No. 55272, Wash., D. C.

Description.—Relatively small dactylogyrid provided with a smooth thin cuticle, length 0.296 mm (0.206-0.486 mm), greatest width 0.054 mm (0.036-0.072 mm) usually present in posterior half of trunk. Eyespots four, members of anterior pair somewhat smaller and farther apart than those of posterior pair; accessory melanistic granules, apparently of same type which comprise eyespots, infrequently present in cephalic region. Cephalic lobes inconspicuous; head organs indistinct. Pharynx spherical-to-subpherical in outline (dorsal view), transverse diameter 0.017 mm (0.016-0.021 mm). Peduncle short-to-elongate; haptor subovate in outline (dorsal view) and broader than long, greatest width 0.055 mm (0.029-0.076 mm), length 0.051 mm (0.029-0.055 mm). Each anchor composed of 1) a base with well-developed superficial and deep roots (former longer), 2) a solid shaft and 3) a solid point (Pl. 2, fig. 45). Anchor wings distinct and bag-like. Anchor length 0.033 mm (0.029-0.037 mm), greatest width 0.016 mm (0.012-0.020 mm). Dorsal bar frequently yoke shaped and somewhat variable (Pl. 2, figs. 41, 42); length 0.028 mm (0.020-0.029 mm). Vestigial ventral bar small and not observed in all specimens, composed of two posteriorly bent limbs and an anteriorly projecting median process (Pl. 2, figs. 43, 44), length 0.016 mm (0.012-0.022 mm). Hooks, fourteen in number, approximately equal in size and normal in arrangement (Mizelle 1938). Each hook consists of 1) a conspicuous base, 2) a slender shaft, and 3) a sickle-shaped termination (Pl. 2, figs. 46, 47). Posteriorly projecting process usually conspicuous and almost as long as the hook shaft. Shafts of hooks usually shorter than base. Hook length 0.019 mm (0.018-0.022 mm). Vitellaria poorly developed and extend from posterior border of pharynx to anterior portion of peduncle. Ovary elliptical in

outline (dorsal view) and pretesticular. Two prostates near base of cirrus, usually laterally displaced; seminal vesicle well developed. Vagina inconspicuous and present on right lateral margin near midlength of trunk. Copulatory complex consists of a cirrus and accessory piece. Cirrus a relatively thick, gently curved tube with expanded tip. Base characterized by presence of an anteriorly projecting digitiform process (Pl. 2, figs. 37, 38); cirrus length 0.035 mm (0.024-0.039 mm). Accessory piece tripartite, attached basally to cirrus, with a membranous flange between lateral extension and distal extremity, lateral extension lies under cirrus (Pl. 2, figs. 39, 40), length 0.026 mm (0.024-0.029 mm).

The closest apparent relative of *D. semotilis* is *D. bulbis* Mueller, 1938. Although the copulatory complexes are similar in these two species (Pl. 2, figs. 37-40; Mueller 1938, Pl. 3, fig. 23) the remainder of the cuticularized structures are strikingly dissimilar Pl. 2, figs. 41-47; Mueller 1938, Pl. 3, figs. 23-27).

UROCLEIDUS DISPAR (Mueller) Mizelle and Hughes, 1938

Synonyms.—*Onchocoleidus dispar* Mueller, 1936; *Haplocoleidus dispar* (Mueller, 1936) Mueller, 1937.

Host and locality.—*Archoplites interruptus* (Girard), Brick Yard Pond, Sacramento, California.

Previously reported hosts and localities.—See Mizelle *et al.* (1955).

Specimens studied.—Three.

Description.—Relatively large dactylogyrid provided with a smooth thin cuticle, length 0.404 mm (0.386-0.468 mm), "0.650 mm," greatest width 0.090 mm (0.072-0.108 mm), "0.086 mm," present in middle portion of trunk. Eyespots four, members of anterior pair smaller and farther apart than those of posterior pair. Accessory melanistic granules not observed. Cephalic region with two lappets, one on each side. Five to six pairs of head organs present and extend from the central cephalic region to lappets; cephalic glands indistinct. Pharynx spherical-to-subspherical in outline (dorsal view), transverse diameter 0.029 mm (0.025-0.034 mm), "0.043 mm." Peduncle short and tapered. Haptor longitudinally oblong, width 0.063 mm (0.051-0.076 mm), "0.057 mm," length 0.080 mm (0.072-0.084 mm), "0.071 mm." Two pairs of anchors present, dorsal pair extremely large, ventral pair much smaller (Pl. 2, figs. 53, 54). Each dorsal anchor consists of 1) a well-defined base with a rudimentary deep root and a well-developed superficial root, 2) a moderately curved hollow shaft, and 3) a moderately recurved point; length 0.080 mm, "0.069," greatest width of base 0.011 mm (0.009-0.012 mm), "0.011 mm." Each ventral anchor consists of 1) a base with a small deep root and a well-developed superficial root, 2) a hollow shaft, and 3) a recurved hollow point; length 0.043 mm (0.040-0.051 mm), "0.036 mm," width 0.012 mm (0.010-0.014 mm), "0.014 mm." Dorsal bar variable, elongate and with expanded rounded ends (Pl. 2, figs. 50, 51); length 0.028 mm (0.026-0.029 mm), "0.023 mm." Ventral bar constricted medially and rounded at each end (Pl. 2, fig. 52), length 0.019 mm (0.017-0.022 mm), "0.036." Hooks fourteen in number and normal in arrangement (Mizelle 1938). Each hook consists of 1) an elongate base, 2) a slender shaft and 3) a sickle-shaped termination with a posteriorly projecting process. Members of pair number five possess a base which is as long as the shaft (Pl. 2, fig. 55); base of other hooks shorter than shaft. Hook length 0.018 mm (0.016-0.020 mm), "0.014-0.017." Vitellaria well developed and extend from posterior region of pharynx to anterior portion of peduncle. Ovary large and located axially in posterior region of body; testis, prostates and seminal vesicle obscured by dense vitellaria. Vagina not observed. Copulatory complex consists of a cirrus and accessory piece. Cirrus a hollow tapering tube with a fine thread wound around the shaft (Pl. 2, fig. 48), length 0.029 mm (0.027-0.031 mm), "0.026 mm." Accessory piece consists of a shaft parallel to cirrus, the end of which bears two processes which encircle extremity of cirrus (Pl. 2, fig. 49).

HOST SPECIFICITY OF THE GENUS GYRODACTYLUS

Host specificity of the Monogenea has been recognized and studied by many authors: Bychowsky (1933a), Nybelin (1937), Mizelle, La Grave, &

O'Shaughnessy (1943), Baer (1951), Hargis (1953), and Monaco & Mizelle (1955). Host specificity is narrowly expressed in some categories as for example the Tetraonchinae in which the species of parasite is indicative of the host species (Mizelle, LaGrave & O'Shaughnessy 1943, Mizelle 1949) whereas it is less marked in the genus *Dactylogyrus* (Monaco & Mizelle, 1955).

In the genus *Gyrodactylus*, 19 families of fishes serve as hosts, with the family Cyprinidae harboring 11 of a total of 26 species.⁵ Monaco and Mizelle (1955) and Bychowsky (1933a) noted that *Dactylogyrus* species could be divided into four groups according to the number of host species parasitized. In the genus *Gyrodactylus*, however, these groups exceed this number (table 1) and no significant pattern is indicated to the present authors. The presence of these forms on the gills, fins, and general body surface of their hosts may indicate less host specificity than in the dactylogyrids which are limited to branchial tissue, but in the present authors' opinion this is not necessarily true because all the species described in the present work were recovered from branchial tissue (skin was not examined).

Of the total 28 known species of *Gyrodactylus*, 78.2% were found on a single host species (table 1). This indicates a much higher host specificity than that observed in the genus *Dactylogyrus* by Monaco and Mizelle (1955). Of the remaining species 6.89% infected three hosts, and 3.44% infected each of the groups 2, 6, 7, 9, and 19 species.

Only *G. elegans* has been recovered from both Old and New World hosts (table 1). It parasitizes 19 species of fish in the Old World and 6 species in the New World. The host list includes 18 genera in 10 families of fishes. This diversity exceeds the range for that of *D. banghami* Mizelle and Donahue, 1944 (Monaco and Mizelle 1955) and it is difficult in light of these two cases (*G. elegans* and *D. banghami*) to postulate a physiological mechanism as proposed by Nigrelli (1937).

TAXONOMIC CONSIDERATIONS

Mueller (1936) described "A" and "B" varieties of "*G. elegans* v. Nordn." and conjectured that he might be dealing with forms which parallel those of the Old World. He also stated that although these variations were small nevertheless they were constant and he therefore erected the varieties "A"

TABLE 1.—Comparative specificity of *Gyrodactylus* species.

	Different host species parasitized							
	1	2	3	6	7	9	19	
North American <i>Gyrodactylus</i> species	15	1	0	1*	0	0	0	
Old World <i>Gyrodactylus</i> species	8	0	2	0	1	1	1*	
Total <i>Gyrodactylus</i> species	23	1	2	1	1	1	1	
	78.2%	3.44%	6.89%	3.44%	3.44%	3.44%	3.44%	

* *Gyrodactylus elegans* v. Nordn., 1832.

⁵ *G. incisura* Ikezaki, 1955, from the skin, gills and fins of *Eucalia inconstans* is as yet unpublished.

TABLE 2.—Comparative body measurements (mm) of
G. elegans v. Nordn. var. A & B Mueller, 1936.

	Body Length	Pharynx Diameter	Cirrus Diameter	Anchor Length	Hooks (entire)
Var. "A"	0.4-0.5	0.035-0.04	0.02-0.025	0.07-0.075	0.03
Var. "B"	0.4-0.45	0.037	0.013-0.017	0.065-0.070	0.048

and "B". Yin and Sproston (1948) gave these varieties of Mueller sub-specific status, naming them *G. elegans muelleri* nom. nov. and *G. elegans salmonis* nom. nov., respectively. Four other species were relegated to sub-specific categories by these authors: *G. elegans* Bychowsky, 1933b, to *G. e. elegans* (v. Nord., 1832); *G. japonicus* Kikuchi, 1929, to *G. e. japonicus* (Kikuchi) comb. nov.; *G. elegans* Yamaguti, 1940, to *G. e. yamaguti* nom. nov. They also described *G. elegans sinicus* as a new subspecies.

It is the opinion of the authors that these varieties and subspecies are not valid and constitute nothing more than normal variation readily recognized in descriptions based on several specimens. Table 2 shows in a comparative way for instance how Mueller's two varieties are identical in that they fall within the normal range of variation.

Until more information is available concerning the actual life cycles and genetics of these forms such taxonomic designations should be withheld.

Several undesigned species of *Gyrodactylus* have been recorded but described poorly. Notably those of Linton (1940),⁶ and Stunkard and Dunihue (1933). Linton in his description records 18 hooks in the haptor, showed 17 in his figure (Pl. 14, fig. 158) while 16 is the characteristic number for the members of this genus. He also recorded 2 spines on the posterior margin of the haptor which were never reported previously or subsequently.

The unusual case of a gyrodactylid occurring on an amphibian host by Stunkard and Dunihue (1933) has not been verified by other workers.

In the course of examining branchial material in the present investigation four new species of the genus *Dactylogyrus* were discovered. The vestigial ventral bar was observed in only two of these species and then in only some of the specimens, which indicates it to be a variable structure. For this reason these species have been placed in the genus *Dactylogyrus* rather than in *Neodactylogyrus* Price (1938). Such structure is considered unreliable for generic recognition and according to Mayr et al (1953) ". . . is not valid for sound taxonomic work."

NORTH AMERICAN GYRODACTYLINAE AND THEIR FISH HOSTS

Gyrodactylus bairdi n. sp.—*Cottus b. bairdi* (Girard), Judy Creek, St. Joseph County, Indiana (pr. auth.).

Gyrodactylus couesi n. sp.—*Couesius plumbius dissimilis* (Girard), Loon Lake, British Columbia, Canada (pr. auth.).

Gyrodactylus cylindriformis Mueller & Van Cleave, 1932.—*Umbra limi* (Kirtland), Oneida Lake, New York (Mueller & Van Cleave 1932).

Gyrodactylus egregius n. sp.—*Richardsonius egregius* (Girard), Lahotan Reservoir, Reno, Nevada (pr. auth.).

⁶ Hargis (1955) described this species correctly and named it *G. prolongis*.

Gyrodactylus elegans von Nordmann, 1832.—*Carassius auratus* (Linnaeus), Ithaca, New York (Var. A) (Mueller 1936). *Samo clarki lewisi* (Girard), *Salmo trutta fario* (Linnaeus) and *Salvelinus f. fontinalis* (Mitchill), State of Washington and Ithaca, New York, (Var. B), (Mueller 1936). *Ameiurus melas* (Rafinesque). Stillwater, Oklahoma (Seamster, 1938). *Lepomis m. macrochirus* Rafinesque, Westhampton Lake, Richmond, Va. (Hargis 1953).

Gyrodactylus fairporti Van Cleave, 1921.—*Ameiurus melas* (Rafinesque), and *Cyprinus carpio* (Linnaeus), Fairport, Iowa (Van Cleave 1921).

Gyrodactylus funduli Hargis, 1955.—*Fundulus similis*, Franklin Co., Fla. (Hargis 1955).

Gyrodactylus gurleyi Price, 1937.—*Carassius auratus* (Linnaeus), Texas (Price 1937).

Gyrodactylus incisura Ikezaki (unpublished).—*Eucalia inconstans* (Kirtland) English Coulee, University of North Dakota campus, Grand Forks, North Dakota. This species has no validity until publication of description.

Gyrodactylus limi n. sp.—*Umbra limi* (Kirtland), Judy Creek, St. Joseph County, Indiana (pr. auth.).

Gyrodactylus micropogonius n. sp.—*Micropogon undulatus* (Linnaeus), Aransas Pass, Texas (pr. auth.).

Gyrodactylus prolongis Hargis, 1955. (Syn. G. sp. of Linton, 1940).—*Fundulus grandis* Baird & Girard, Franklin Co., Fla. (Hargis 1955).

Gyrodactylus rhinichthius n. sp.—*Rhinichthys osculus robustus* (Rutter), Lahotan Reservoir, Reno, Nevada (pr. auth.).

Gyrodactylus richardsonius n. sp.—*Rhinichthys osculus robustus* (Rutter), Lahotan Reservoir, Reno, Nevada (pr. auth.).

Gyrodactylus spathulatus Mueller, 1936.—*Catostomus commersonii* (Lacépède), Ithaca, New York (Mueller 1936).

Gyrodactylus stegurus Mueller, 1937.—*Fundulus diaphanus* (LeSueur), Constantia, New York (Mueller 1937).

Gyrodactylus stephanus Mueller, 1937.—*Fundulus heteroclitus* (Linnaeus), Baltimore, Maryland (Mueller 1937). *Fundulus grandis* Baird & Girard, Alligator Harbor, Fla. (Hargis 1955).

NORTH AMERICAN FISH HOSTS AND THEIR GYRODACTYLIDS AMEIURIDAE

Ameiurus melas (Rafinesque)—*G. elegans* von Nordmann, 1832; *G. fairporti* Van Cleave, 1921.

CATOSTOMIDAE

Catostomus commersonii (Lacépède)—*G. spathulatus* Mueller, 1936.

CENTRARCHIDAE

Lepomis macrochirus Rafinesque—*G. elegans* von Nordmann, 1832.

COTTIDAE

Cottus b. bairdi (Girard)—*G. bairdi* n. sp.

CYPRINIDAE

Carassius auratus (Linnaeus)—*G. elegans* von Nordmann, 1832; *G. gurleyi* Price, 1937. *Couesius plumbeus dissimilis* (Girard)—*G. couesi* n. sp. *Cyprinus carpio* (Linnaeus)—*G. elegans* von Nordmann, 1832; *G. fairporti* Van Cleave, 1921. *Rhinichthys osculus robustus* (Rutter)—*G. rhinichthius* n. sp. *Richardsonius egregius* (Girard)—*G. egregius* n. sp.; *G. richardsonius* n. sp.

CYPRINODONTIDAE

Fundulus diaphanus (LeSueur)—*G. stegurus* Mueller, 1937. *Fundulus grandis* Baird & Girard—*G. prolongis* Hargis, 1955. *Fundulus heteroclitus* (Linnaeus)—*G. stephanus* Mueller, 1937. *Fundulus similis* (Baird & Girard)—*G. funduli* Hargis, 1955.

GASTEROSTEIDAE

Eucalia inconstans (Kirtland)—*G. incisura* Ikezaki.*

SALMONIDAE

Salmo clarki lewisi (Girard)—*G. elegans* von Nordmann, 1832. *Salmo trutta fario* (Linnaeus)—*G. elegans* von Nordmann, 1832. *Salvelinus f. fontinalis* (Mitchill) *G. elegans* von Nordmann, 1832.

SCIAENIDAE

Micropogon undulatus (Linnaeus)—*G. micropogonus* n. sp.

UMBRIDAE*

Umbra limi (Kirtland)—*G. cylindriformis* Mueller & Van Cleave, 1932; *G. limi* n. sp.

SUMMARY

Seven new species of *Gyrodactylus* and four new species of *Dactylogyrus* are described from gills of fishes from British Columbia, California, Indiana, Michigan, Nevada, and Texas: *G. egregius* n. sp., *G. richardsonius* n. sp., from *Richardsonius egregius* (Girard); *G. rhinichthius* n. sp., *D. osculus* n. sp. from *Rhinichthys osculus robustus* (Rutter) all (4) from Nevada; *G. bairdi* n. sp. from *Cottus b. bairdi* Girard, *G. limi* n. sp. from *Umbra limi* (Kirtland), *D. rhinichthius* n. sp. from *Rhinichthys atratulus meleagris* (Agassiz), all (3) from Indiana; *G. couesi* n. sp. from *Couesius plumbeus dissimilis* (Girard) from British Columbia, Canada; *D. semotilis* n. sp. from *Semotilis a. atramaculatus* (Mitchill) from Michigan; *G. micropogonus* n. sp. from *Micropogon undulatus* (Linnaeus) and *D. nuchalis* n. sp. from *Hybognathus n. nuchalis* Agassiz, both from Texas. *Urocleidus dispar* (Mueller) Mizelle and Hughes (1938) is comparatively described because of its occurrence on *Archoplites interruptus* (Girard) the only native centrarchid west of the Rocky Mountains, which constitutes a new host record.

A table of *Gyrodactylus* species and the different hosts infested by each, shows that 78.2% infest one host each, 6.89% infest 3 host species and 3.44% infest each of two, six, seven, nine, and nineteen different host species. This data shows that the host specificity among the *Gyrodactylinae* is much more limited than in the *Dactylogyrinae* (Monaco and Mizelle 1955).

A standard terminology for description of *Gyrodactylus* species is proposed.

The subspecific categories of *Gyrodactylus* erected by Yin and Sproston (1948) are hereby rejected for lack of adequate studies on this group.

The genus *Neodactylogyrus* Price, 1938, is considered invalid.

North American species of *Gyrodactylus* are listed with the hosts infested and other pertinent data.

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* This description of this species is unpublished and therefore has no validity at present.

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Boreal Hepaticae, a Manual of the Liverworts of Minnesota and Adjacent Regions

II. Ecology*

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The Region Treated

Although this work deals nominally with the Hepaticae of Minnesota, political boundaries impose no intrinsic compunctions on a group of plants to show similar limits; use of such boundaries is therefore rather meaningless. In almost all cases, the species treated herein have an infinitely broader distribution; hence this work should be of use to students throughout much of the northeastern portion of the United States, as well as the southern half of Ontario and Quebec.‡

Four major vegetational types are recognizable among the Hepaticae treated: arctic-alpine elements, showing the the bulk of their distribution in

* The initial, taxonomic section of this work appeared in *THE AMERICAN MIDLAND NATURALIST* 49(2) :i-v, 257-684, 1953.

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The major work on this section was done during 1947-1950, while the writer was at the University of Minnesota; revisions of portions of the manuscript were made at Duke University. In addition to the acknowledgements made in Part I. (p. 259), I would wish to further express my appreciation to Dr. H. Buch and the late Dr. K. Müller for their critical examination of a number of specimens submitted to them, and to Dr. L. E. Anderson, for a reading of portions of the manuscript. Any errors of omission or commission are, however, to be attributed to the author. I must again acknowledge the aid of my wife, Olga M. Schuster, particularly with preparation of the manuscript for publication. Finally, two National Science Foundation Grants (Grants 669 and 1396) and a Guggenheim Fellowship for the year 1955-56 have made possible some of the time needed for the final work on this manuscript, and have made possible field work which considerably broadened the scope of this work. I would like again to stress the fact that the necessity of writing for a group of students ranging from relative beginners to specialists has meant inclusion of materials at once too complex for the beginner and too elementary for the specialist. In order not to lose too much continuity, the more technical material has, in general, been placed either in footnotes or in smaller type in the text.

‡ All of the species known from the Dakotas, from southern Ontario, Wisconsin, Iowa, Michigan, and Illinois have been included in the systematic portion (*Amer. Midl. Nat.* 49(2) :i-v, 257-684, 1953); over 90% of the species found in each of these states have also been found in Minnesota. Circa 75-90% of the species occurring in New York, Ohio, Indiana, Connecticut, Pennsylvania, Missouri, Nebraska and Kansas are treated in the present work. The wide distribution of most of the species covered in this text is also readily evident from inspection of figs. 40-82, in which the North American range of various species is depicted.

the treeless regions of the north, or on barren mountain summits (i.e., in the Tundra); subarctic-subalpine elements, with the bulk of their distribution in the boreal, cold, Coniferous Forests (i.e., species occurring essentially in the Taiga, with a Hudsonian-Canadian distribution, using the terminology of Merriam); Deciduous Forest types, occurring essentially south of the borders of the Coniferous Forest Region; Prairie types, limited largely to the treeless regions of low rainfall.

The Tundra species occurring in Minnesota and adjacent regions are relatively limited; such typical Tundra taxa as *Tennoma setiforme* and *Gymnomitrion concinnatum* do not occur. However, other, equally northern types do occur as "relicts," such as *Lophozia quadriloba*, *L. atlantica*, *Anthelia juratzkana*, and *Scapania degenii*, etc. Therefore, the Tundra elements are treated only to a partial degree. The Prairie, except for the postclimates along river-courses, is virtually devoid of Hepaticae (except for members of the Ricciaceae); since the postclimates show attenuated hepatic stratal societies allied to those of the Deciduous Region, the Prairie is not treated in detail here. The present work, therefore, deals largely with the Northern Coniferous and Eastern Deciduous Formations.

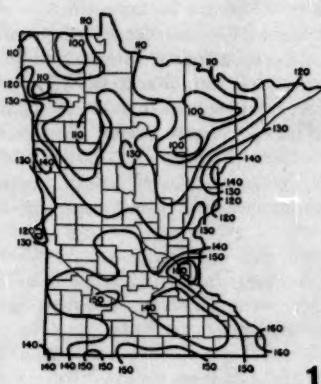
PHYSICAL AND GEOLOGICAL FEATURES

Minnesota lies in a region with a growing season of 94-162 days.* That area with a growing season of approximately 94-125 days is covered largely with coniferous forest; this region has in general an adequate, if not copious, precipitation (22-30 in.). The area with a growing season of 125-162 days is covered eithered by deciduous forest or by prairie. In the Deciduous Forest Region the precipitation varies from a rather moderate 32 in. (in the southeast) to as little as 20-22 in. (in the northwest); as one goes northward, a decreased precipitation tends to remain sufficient because of the colder climate and lower evaporation rate.

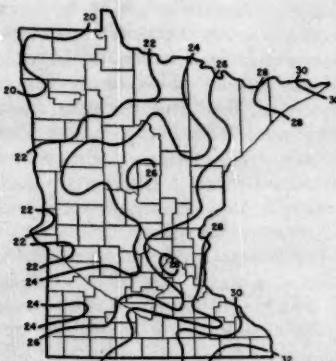
The highest precipitation (30-32 in. per year) occurs in the northeastern and southeastern corners of the state, while the precipitation remains "adequate" (25-28 in.) along the eastern border of the state between these upper and lower extremes. This high precipitation rate in the northeastern and southeastern corners of the state is graphically correlated with the richness of the hepatic flora.† As one goes westward, the precipitation drops off:

* This is approximately the same (slightly less) than for central and western New York (see Schuster, 1949). The rather pronounced differences in vegetation between the two regions as regards both the dominant forest species and the Hepaticae, are quite striking. This suggests that length of the growing season, by itself, is almost meaningless in distinguishing vegetational regions.

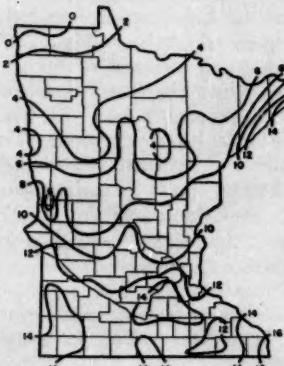
† At least 122 species are known from Cook County, in the northeastern corner of the state, where we have a low temperature, high moisture (due to juxtaposition to a large body of water), and high precipitation. Similarly, about 40 species are known from Houston and Winona cos. together (of almost equal area, taken together, as Cook Co.): a very high number of species, when we consider that only a portion of these counties is wooded. The very high number of species in Cook Co., adjacent to Lake Superior, is also partially explicable on the basis of the tempering effect of Lake Superior on climatic extremes. It is to be noted from Text figs. 19-20 that the average January temperature in the area adjacent to Lake Superior is 14° F (only 2° less than the maximal average January temperature recorded only for the southeastern extreme corner of the state, in Houston Co.) while the July temperature averages less than 58° in the extreme northeastern corner of Cook Co., with the probable actual average temperature of the area adjacent to the lake shore probably less than 55° in such places as the Susie Islands, which are completely surrounded by lake water. In such areas we therefore have a lesser



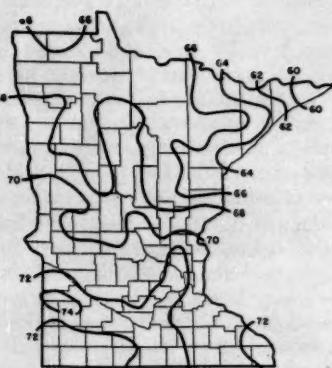
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Figs. 17-20.—Climatic maps of Minnesota (from U.S.D.A. Yearbook, *Climate and Man*). 17. Average number of days without killing frost; 18. Average annual precipitation; 19. Average January temperature; 20. Average July temperature.

difference between the January and July averages ($41-46^{\circ}$), with the extreme temperatures also probably reasonably low. In the western portions of the state, on the other hand, we find a much more continental climate, with the January-July averages differing by 60.74° , locally even more. In the northeastern extreme of the state we thus find relatively oceanic climatic conditions, both as regards relatively adequate precipitation, and absence of climatic extremes—especially in the absence of very high summer temperatures. This contrasts very strongly with the continental climate prevailing over almost all of the rest of the state, and goes far to explain the tremendous differences in the degree of development of the bryophyte flora. If the Distribution Maps are compared with figs. 18-20, the graphic correlation between low summer and relatively high winter temperatures, and high precipitation and a high incidence of hepatic species (as well as their numerical abundance, which, of course, can be estimated only very roughly from the number of distribution dots) becomes self-evident.

averaging from 18 to 20 in. in the north to 22-26 in. in the south (where temperature and the evaporation rate are higher). This precipitation, over most of this area, is hardly adequate to support a forest biome; correlated with the absence of forests we find that Hepaticae are almost lacking along the western border of the state (except for a few species that occur in the Cottonwood-Willow-Elm-Hackberry Postclimax Forests along the river-courses). It is therefore evident that the continental climate of the state exerts a profound effect on the over-all distribution of such delicate, generally mesophytic plants as Hepaticae. Only the xeromorphic Ricciaceae represent an exception to this rule.

Differences in elevation clearly influence the distribution of Hepaticae in montane areas. Since Minnesota is, by and large, a plateau at the head of the Mississippi River, with an elevation of some 1200 ft., elevation is a negligible feature. The relief is at best moderate: extremes in elevation range from 2,230 ft. in the Misquah Hills of Cook Co., to the border of Lake Superior, which is merely 602 ft. This difference in itself is scarcely meaningful as an influence governing the distribution of the larger dominant plants. Both the region adjacent to the shores of Lake Superior and the Misquah Hills bear a coniferous forest of great similarity. The distribution of the Hepaticae, however, follows no such simple pattern.*

We are accustomed to a distribution pattern where the most "northern" species occur at the summits of the highest elevational points, the most southern species being restricted to the regions with lowest elevation. The distribution of the Hepaticae normally also follows this pattern.† However, there is a superficially anomalous inverse distribution of the Hepaticae (and of many of the smaller ferns) in Minnesota: the most "northern" and "arctic-alpine" species are restricted to within a few feet of the shore of Lake Superior—at an elevation of less than 650 ft.; all of these notably northern elements are lacking in the regions with an elevation of over 1200 ft. This seemingly anomalous distribution is due to the influence of Lake Superior, which exerts a profound effect on the nature of the flora immediately along its shores. The effects of the lake will be discussed in detail.

Finally brief consideration of the rock-outcrops is needed for an understanding of the distribution pattern exhibited by the Hepaticae within the state. One of the important features of the underlying rocks and exposed rocks lies in the fact that truly acidic rocks are quite rare; hence the species which we generally find common in regions with crystalline, igneous or metamorphosed acidic rocks are local or nearly absent: among them such species as *Mylia taylori*, *Marsupella sphacelata*, *M. emarginata*, *Scapania paludosa*, and *Solenostoma cordifolium*. Other species more abundant in regions with siliceous rocks are of restricted distribution: *Diplophyllum taxifolium*, *Anastrophyllum michauxii*, *Lophozia alpestris*, *Cephalozia leucantha*, *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Gymnocolea inflata*, *Scapania umbrosa*,

* This is due to the fact that microdistribution is extremely significant in governing the distribution of such small plants, occupying restricted sites, as the bryophytes.

† As is evident from the discussion of the distribution pattern in central and western New York (Schuster, 1949).

etc. (Some of these species, however, are Oceanic or Suboceanic in range).

The existing rock-outcrops consist, in the southeastern region, largely of calcareous and subcalcareous sandstones, forming the extensive bluffs along the Mississippi River and Minnesota and St. Croix rivers. The friable and basic nature of these rocks decidedly restricts the nature of the Hepaticae that occur. Such types as *Reboulia*, *Preissia*, *Clevea*, *Mannia rupestris*, *Frullania riparia*, *Plagiochila asplenoides*, *Lophocolea minor*, *Lophozia* (*Leiocolea*) *mulleri*, *Chiloscyphus pallescens*, and *Riccardia pinguis* (i.e., either decided "calciphiles" or decidedly lime-tolerant species) being predominant. Some of these species extend northward approximately to the region where these basic sandstones end: i.e., to about Taylors Falls, along the St. Croix River and Minneapolis, along the Mississippi River, but no further.

In the northeastern third of the state, especially along the shore of Lake Superior, the rocks are of Algonkian age. They are often largely basaltic (diabasic), with local outcrops of calcareous shales and slates (the Rove Slate) adjacent to the Canadian border in northeastern Minnesota (Grout and Schwartz, 1933, 1939; Gruner, 1941; Butters and Abbe, 1953). These rocks are almost all slightly to distinctly basic, i.e., with calcium and magnesium, rather than potassic and siliceous rocks. The basic nature of these rocks (with localized outcrops of calcite, barite and similar minerals) has a decided influence on the nature of the hepatic flora. As stated above, the decidedly "calciphobe" species are rare or absent as pioneers on rocks; their place is often taken by a notable group of "calciphile" and "tolerant" species, such as *Tritomaria quinquedentata*, *T. scitula*, *Plagiochila asplenoides*, *Preissia quadrata*, *Scapania gymnostomophila*, *S. cuspiduligera*, *S. nemorosa*, *S. degeneri*, *Lophozia* (*Leiocolea*) *gillmani*, *L. schultzii*, *L. badensis*, *L. heterocolpa*, *L. grandiretis*, *Odontoschisma macounii*, *Pellia fabroniana*, *Mannia pilosa*, *Asterella ludwigii*, etc. The predominant occurrence of these species gives the entire "North Shore" of Lake Superior a floral spectrum that is decidedly restricted to areas with basic rock-outcrops. A limited region adjacent to Canada, centering around Saganaga Lake, has largely Archean siliceous rocks (Saganaga granite). This area, unfortunately, has not yet been studied by the writer.

According to the most recent geological evidence, all or virtually all of Minnesota was glaciated during the Pleistocene. A narrow strip in southeastern Minnesota, ranging from Winona Co. south into Houston Co.* has been very generally regarded as unglaciated. Again, cumulative botanical exploration during the last century in or near the northeastern corner of the state has suggested "imperfect" glaciation may have occurred in this general region (Hultén, 1937; Fernald, 1935). Agassiz (1850) found floristic disjuncts in the Thunder Bay and Algoma regions of adjacent Ontario; Juni (1879) and Roberts (1880), and more recently Butters and Abbe (1953) have extended many of these south into our area, adding others. Similarly, Cooper (1913) and Brown (1937) reported many such disjuncts from adjacent Isle Royale. It therefore could be (and has been) postulated,

* At least the summits of some of the taller bluffs in the area appear to have truly escaped recent glaciation. On some of them I have seen no trace of erratic boulders, and the upper portions of these bluffs are notable in that they form the sites for such "disjunct" and essentially arctic-alpine relict species as *Clevea hyalina*, *Asterella saccata*, *Mannia sibirica*. The disjunct nature of the distribution of these species strongly suggests that at least portions of the bluffs on the Minnesota side of the Mississippi River must have escaped all trace of recent glaciation.

on phytogeographical grounds, that small areas in this general region may not have been fully covered by the ice sheets of the Pleistocene at one time (Hultén, 1937); included possibly is a small area in northeastern Minnesota, which we may call the "Arrowhead Enclave," thus allowing a hypothetical group of more or less pioneer species to survive there. These species are known to tolerate periglacial climates, therefore could have shifted rapidly with the local recession and advance of the ice-sheet and quickly occupied local sites of raw earth or rock that had been freed of ice.

The occurrence in that area of a number of "disjunct" species, such as *Asterella ludoviciana*, *Mannia pilosa*, *Scapania degemii*, *Tritomaria scutula*, *Scapania cuspiduligera*, *Cryptocolea imbricata*, all of which are often pioneers, and all of which are decided "calciphiles" is suggestive: the restricted distribution (in Minnesota) of most of these to the periphery of the Arrowhead Enclave is perhaps no fortuitous accident. Neither, perhaps, is the recurrence of many of these species on the Keweenaw Peninsula of Michigan, which has been hypothesized as an Enclave or "Nunatak Area." According to recent geological evidence, however, the Cary glaciation in Cook County was complete, glaciation extending roughly to the southwest, but the "Rainy Lobe" receded at an early date, with a lobe to the east ("Superior Lobe") active soon thereafter. With the recession of the Rainy Lobe, the Superior Lobe on the east and a St. Louis Sublobe to the west extended southward, meeting to the south of the "Arrowhead" Region. These two advancing glacial lobes, together with the retreating Rainy Lobe, thus delimited an ice-free triangular region between them. This ice-free area, dating back at least 11,000 years (Flint and Deevey, 1951), may, according to Butters and Abbe (1953), have extended back as much as 20,000 years. Thus parts of Cook and St. Louis counties may have been free of continental ice for a much longer period than the immediately surrounding areas, even if this hypothetical "enclave" was fully glaciated at an earlier time. See in this connection Butters and Abbe (1953, pp. 29-33).

With the possible exception of these two very restricted regions, all of the flora of the state is clearly the result of postglacial migration back to a region that was wholly covered with a thick ice-sheet. Such zonation as exists in the distribution of the Hepaticae is thus generally of postglacial origin, with the possible exception of portions of the vegetation of the northeastern corner, and of the southeastern corner (whose disjunct nature suggests that their existing distribution is preglacial or Pleistocene in origin).

OUTLINE OF DEVELOPMENT OF THE PRESENT VEGETATION*

In any consideration of the existing vegetational elements represented by the Hepaticae occurring in Minnesota (which will be considered in the next section), the historical background of the flora must be considered.

As has been stressed above, localized lack of recent glaciation (or the retention of fluctuating enclaves in which invading species could survive) has probably been critical in explaining some of the diversity of vegetational elements represented by the Hepaticae found in the state.

We know that immediately preceding the Wisconsin glaciation, the flora of Minnesota was apparently very similar to that occurring at present. During the period of glaciation, this boreal and temperate flora was forced southward and exterminated northward. The Coniferous Zone elements were forced southward far south of where they occur today, and were probably surrounded by a narrow Tundra Zone at the edge of the ice-sheet. The

* The historical implications of the existing vegetation are dealt with in detail under Phytogeography. The present sketch merely attempts to set the stage for the discussion on ecology that follows.

Tundra, Coniferous Region, and zone of Deciduous Forests were very probably much more tightly compressed together: with the Coniferous and Deciduous Forests quite mixed and interdigitated.*

The only local area where this closely interdigitated complex of vegetational elements was able to survive regionally was in a small section along the Mississippi River, along the southeastern border of the state, and to the east in Wisconsin. This so-called "Driftless Area" is extremely significant in explaining some of the anomalies in distribution that some species found in the state exhibit.

This Driftless Area still is the home today (in Minnesota and in adjacent Wisconsin) of such northern vascular plants as *Potentilla tridentata*, *Primula mistassinica*, *Sorbus dumosa*, *Lycopodium annotinum*, *Thuja occidentalis*, *Abies balsamea*, *Taxus canadensis*, etc. In addition, such Arctic-alpine Hepaticae as *Clevea hyalina*, *Mannia sibirica*, and *Astrella saccata* persist there. Some of these species conceivably survived the Pleistocene in this Driftless Area of the southeastern portion of the state, and in adjacent parts of Wisconsin and Illinois. The restricted distribution of some species that today occur abundantly in the Lake Superior area can perhaps be traced back to this survival in an enclave directly south of the lake. Among these species are such Hepaticae as *Mannia sibirica* and *pilosa*, and such vascular species as *Mertensia paniculata* and *Potentilla tridentata*. This phenomenon is discussed in detail subsequently.

The magnitude of the effect on the existing Lake Superior vegetation of this "reservoir" population in the Driftless Area is not clear; it may have been negligible. The bulk of the vegetation, both of Hepaticae and of other plants, certainly is the result of several migratory waves that invaded the area from the east and west, as well as from the south, repopulating the recently ice-free, raw soils freed by the recession of the ice-sheet. In this early resettlement, Hepaticae (and mosses) definitely played an important part, because of their pioneer nature, their small size, and their known ability to undergo ecesis in close juxtaposition to the ice-fields—as well as their ability to exist under periglacial conditions, where the annual snow and ice-cover persist for very long periods of time into the short summer that must have then existed. Such local "relict" species as *Anthelia juratzkana*, *Lophozia alpestris*, *Solenostoma schiffneri*, *Odontoschisma macounii*, *Cryptocolea imbricata*, *Lophozia latifolia*, *L. quadriloba* and *L. groenlandica* still exist today on sites in the highest mountains where ice and snow persist until July and where there is less than a sixty day growing season (as on the summit of Mt. Katahdin and in northern Ellesmere Island).†

* This interdigitated nature of the northern Deciduous Forests and Coniferous Forests still persists today to some degree: the so-called Northern Hardwoods Forest (Lake Forest of Weaver and Clements), consisting of conifers (White Pine, Hemlock) mixed with Deciduous trees (Yellow Birch, Maple, Basswood, etc.) is considered by some as a broad "ecotone area" between the true Coniferous and Deciduous Forests.

† All eight of these species, locally of "relict" occurrence, were found by the writer during the summer of 1955 in northeastern Ellesmere Island, at latitude 82°25'-82°32' North, ca. 520 mi. from the North Pole. Several of these species, in fact, were frequent to abundant components of the high-arctic tundra of that area. Among them are *Cryptocolea imbricata* Schuster and *Lophozia latifolia* Schuster, two species described from single stations each, from the Lake Superior area, in the first section of this work. The *Anthelia*, the *L. quadriloba*, and the *Cryptocolea*, furthermore, occurred at times in areas where permafrost was never more than 2-4 in. below the surface.

A third possible factor should finally be considered, in addition to the reinvasion from the Driftless Area and reinvasion along the retreating or oscillating ice-fronts: namely localized survival in, or very early reinvasion into oscillating or fluctuating enclaves—specifically in a hypothetical Arrowhead Enclave (see discussion in Butters and Abbe, 1953). Such a small enclave, reduced entirely to raw soil and raw rock outcrops, could certainly have served as a refugium for bryophytes, since these are ideally at home on such raw sites where competition is low. Hepaticae and mosses possess sufficient "motility" so that they could have persisted in such a region with shifting glaciation.*

Historically, therefore, the complex nature of the hepatic (and other) flora of the area appears to have had its source in localized survival in the known enclave of the southeast (the Driftless Area), as well as in a possible early reinvasion into a hypothetical fluctuating enclave in the northeastern portion of the state—with subsequent general reinvasion of the regions eventually freed from ice. The third (and surely most important factor) in the reinvasion of the area was migration east and westward along the recently freed, bare, raw borders of the retreating glaciers, as well as, of course, general reinvasion from the south as the ice retreated northward. These three factors—whatever may have been their individual effects—together go far to explain the phytogeographically rather complex recent flora of the region. A very few species of southern affinity (*Riccia trichocarpa*, *R. dictyospora*, *R. austini*) may be very recent immigrants from the southwestern, unglaciated area. They may not have arrived until the relatively recent "thermal maximum" of 3000-6000 years ago.

Ecology

The biological interrelationships of the Hepaticae are a little-investigated subject. The present discussion is derived largely from the species as they occur locally, hence the succeeding discussion of hepatic "societies" will not always be equally applicable under other climatic conditions.

The "niches," or sites, to which a species is restricted is the result of the interoperation of the environmental factors. The essentially extrinsic features (such as the light, moisture and temperature factors) that determine the occurrence and frequency of a particular species (or society of species) are in addition to such poorly understood, intrinsic, physio-genetic features of a species as its ability to compete, its "toleration," its innate reproductive potential, etc. Almost nothing about these latter factors is known, so we shall not discuss most of them further. As a single example of differences in physiological resistance to drought and dessication, the experimental work of both Höfle (1942, et seq.) and Clausen (1952) may be cited, in which are demonstrated extreme differences between species, and sometimes between popula-

* In this connection it must be emphasized that proof of pleistocene glaciation (such as erratics or glacial striae), is not necessarily proof that the entire area was glaciated at one time. A given region could, conceivably, have been wholly glaciated during the Pleistocene, yet, at any given time, remained partially ice-free. There are, therefore, ramifications to the Fernaldian "Persistence Theory" which are not wholly met by the numerous recent critics of this theory.

tions within the species, in what may be loosely called "toleration" to drought.

The following discussion, therefore, will be limited to an account of the factors that circumscribe the occurrence of our local Hepaticae, i.e., a discussion of the environment that operates on the species. This will be followed by a short discussion of the resulting communities that occur.

These cryptogamic societies include not only Hepaticae (which may in fact be but a small element), but also mosses, various algae, occasionally myxomycetes, and other small organisms such as collembola and rotifers. Space prevents our considering these other organisms here. The societies which we shall treat are all "unistratal" societies, that is to say, they occupy only a single stratum within the larger associations in which they are found. For these micro-associations, or "communities," the term "Assocule" (coined by Clements, 1936; see discussion by Richards, 1938, Schuster, 1949), and for local variants of these assocules, the term "facies" will be used. Other terms that have been used for unistratal communities are synusia, union, lamiae. Gleason (1939) defines a synusia or union as a "group of plants whose physiological demands are so similar that they are regularly selected by the same environment and regularly live together."

It must also be recognized that the layer-societies, like other communities, can effectively change their environment. Often this modification is so extreme that it automatically puts a temporal limit on the occurrence of a particular community in any one place. Several obvious examples follow: On decorticated, decaying logs the *Nowellia-Jamesoniella* Assocule that undergoes ecesis at an early stage in decay undoubtedly aids in the disintegration and conversion to humus of the substrate; with such decay and modification of the site, other species are able to undergo ecesis and replace the *Nowellia-Jamesoniella* Assocule, since the latter is no longer able to effectively compete under the changed conditions. On such very decayed logs species such as *Calypogeia meylanii*, *Bazzania trilobata*, *Dicranum*, and many pleurocarpous mosses invade; i.e., the corticolous society is supplanted by a humicolous society. Succession is therefore from an epixylic to a bryochamaephytic community. Similarly, on rock-walls we may have an initial invasion of algae and lichens, followed by one phase or another of the "pioneer" epipetric *Lophozia-Scapania* Assocule. With the formation of a thick mat of these species a soil layer is formed by the decay of the older, decaying portions of the plants. This accumulated soil layer may result in evolution of a chasmophytic or exochamophytic society (where the amount of soil accumulating is limited by slope) or, a helophytic society (where the peaty soil accumulating is not washed away or subject to removal).

It is therefore obvious that, in addition to such "internal" succession as may occur within a society, there is a larger, more important succession of one community by another. This succession, to a large degree, is due to the actual effect of the species on the environment: the ability of a species to compete favorably on a site remaining unchanged essentially only while that site remains unmodified by the physiological activities of the plants. We therefore deal with a dynamic system, and in attempting to define "communities," we are merely taking the more readily distinct stages in succession and circumscribing them. Since the replacement or succession of one group of species by the next is essentially a continuous process, complete intergradation from one community to the next inevitably occurs, until the hypothetical stable climax stage is reached. The micro-communities we deal with thus vary in time. Since the environment is normally not a series of sharply isolated niches, each with unvarying and discrete limits, it follows that the communities are not sharply circumscribable units, and that they lack absolute, discrete limits; they thus vary in space, often within narrow limits. This may be illustrated best if we examine the associated table, in which variation in the *Nowellia-Jamesoniella* community of moist decaying logs is studied, on the basis of presence, not dominance (table 1).

TABLE 1.—Presence of a series of species of Hepaticae on shaded, moist, decaying logs (within the spruce-fir forest). *Lophozia ascendens* Facies of *Nowellia-Jamesoniella* Associale

	Maine (Schuster 17014)	Maine (Schuster 17040)	Maine (Schuster 17015)	(Schuster 17038)	Michigan (Schuster 16101 & ¹ 16104)	(Schuster 17429 & ² 17304)	(Schuster 17329 & 17396)	(Schuster 17304a & 17398)
<i>Lophozia ascendens</i>	x	x	x	x	x	x	x	x
<i>Jamesoniella autumnalis</i>	x				x	x	x	x
<i>Nowellia curvifolia</i>	x				x		x	
<i>Pilidium pulcherrimum</i>						x	x	
<i>Blepharostoma trichophyllum</i>	x		x		x		x	
<i>Lophozia longidens</i>	x			x		x	x	
<i>Lophozia porphyroleuca</i>	x	x		x		x		
<i>Lophozia incisa</i>				x				
<i>Anastrophyllum hellerianum</i>					x	x	x	x
<i>Scapania apiculata</i>					x			
<i>Scapania glaucocephala</i>								
<i>Scapania umbrosa</i>								
<i>Tritomaria exsectiformis</i>					x		x	x
<i>Scapania nemorosa</i>					x			
<i>Cephalozia media</i>		x	x				x	
<i>Cephalozia bicuspidata</i>					x			
<i>Calypogeia suecica</i>		x	x			x	x	
<i>Anastrophyllum michauxii</i>								
<i>Lepidozia reptans</i>						x	x	
<i>Geocalyx graveolans</i>		x				x	x	x
<i>Lophocolea heterophylla</i>					x	x	x	x
<i>Jungermannia lanceolata</i>		x		x		x	x	x
<i>Marsupella ?emarginata</i>								
<i>Riccardia latifrons</i>				x	x		x	

It is evident from this table that there is an enormous amount of variation in the *Nowellia-Jamesoniella* community. Some of this is due to the various degrees of internal succession, i.e., the societies studied are of various ages. There is also a great deal of variation in the number and kind of species present due partly to a "chance factor."

The constitution of many societies is influenced by a final factor that is so obvious it is often ignored: the ability of some of the potentially constituent species to get there. This is due, in part at least, to such internal biotic factors as the reproductive capacity (number of spores or gemmae produced and the efficiency with which these are disseminated) and the actual rarity of the species. A single example here will suffice: The *Lophozia-Scapania* Associale consists of a large number of species, one of the constituent species thereof being *Anastrophyllum saxicolum*. Yet the latter occurs as a member of this Associale but a single known time in Minnesota, the species being extremely rare.¹ The rarity is at least in part the result of its low reproductive potential, since it is almost con-

¹ Also with *T. exsecta*, *T. quinquedentata*, *Odontoschisma elongatum*, *Scapania irrigua*; unusual site at bog margin.

² Also with *Cephalozia rubella* (near var. *sullivantii*).

* In Part I of this work the first station for the species was reported; I have since found it a single time on Mt. Katahdin, Maine. The nearest other station is on James Bay, on Hudson Bay. See fig. 67.

TABLE 1.—(continued)

	(Schuster 17304 ^a & 17398)	Minnesota (Schuster 8001a)	New Hampshire ³ (Lorenz)	(Schuster 17980a)	New York (Wilson)	Wisconsin (Schuster 17523 ^a & 17552)	Ontario (Cain 2448)
<i>Lophozia ascendens</i>	x	x	x	x	x	x	x
<i>Jamesoniella autumnalis</i>	x	x	x			x	x
<i>Nowellia curvifolia</i>	x		x		x	x	x
<i>Ptilidium pulcherrimum</i>		x				x	x
<i>Blepharostoma trichophyllum</i>	x						x
<i>Lophozia longidens</i>							
<i>Lophozia porphyroleuca</i>			x	x	x		
<i>Lophozia incisa</i>							
<i>Anastrophyllum hellerianum</i>	x	x				x	x
<i>Scapania apiculata</i>		x	x				
<i>Scapania glaucocephala</i>		x	x			x ⁴	
<i>Scapania umbrosa</i>				x	x		
<i>Tritomaria exsectiformis</i>	x					x	
<i>Scapania nemorosa</i>							
<i>Cephalozia media</i>							
<i>Cephalozia bicuspidata</i>				x	x		
<i>Calypogeia suecica</i>	x				x		
<i>Anastrophyllum michauxii</i>			x				
<i>Lepidozia reptans</i>	x	x					
<i>Geocalyx graveolans</i>							
<i>Lophocolea heterophylla</i>	x	x				x	
<i>Jungermannia lanceolata</i>	x					x	
<i>Marsupella ?emarginata</i>				x			
<i>Riccardia latifrons</i>							

stantly sterile and has no known asexual means of reproduction, in addition to which it is dioecious (the regional plants are all female). In contrast, *Lophozia ventricosa* (and *L. silvicola* and *L. longidens*, which often replace it) and *Scapania nemorosa*, common and dominant members of this community, reproduce freely by both spores and gemmae.

The structure of the bryophyte community therefore is influenced by a number of factors, among them a series of internal phenomena: 1) The ability of the various members to get to the site. 2) Internal competition within the society. 3) The age of the society and the extent to which the society has modified its environment. 4) The relative intrinsic rarity of the various species belonging to the society. 5) The time at which the various members arrive at the niche under discussion. There is, in addition, an entirely external phenomenon that often modifies the form and composition of the society, namely succession of the larger plants (trees, shrubs, etc.) that may totally change the microenvironment of the unistratal bryophyte communities. For example, both saturation-deficit and light intensity may sharply decrease with increase in density of the larger plants.

Succession is such a complex phenomenon, conditioned by so many factors, that it is often impossible to clearly perceive the direction in which it progresses, unless studies are

³ Also with *Harpanthus scutatus*.

⁴ *Scapania saxicola*, a close relative of *S. glaucocephala*.

carried on for extensive periods of time. Much successional data is based largely or entirely on inferences. Since it is quite impossible, with our present knowledge, to consistently treat the unistratal societies in which Hepaticae play a large part in a dynamic fashion, they will be treated largely statically, based on their essential structure and occurrence.*

AUTECOLOGY

In the study of any group of species, we find that their environment has circumscribed their distribution (both in space and in time); it has also resulted in the selection of various adaptations, both of a physiological and morphological nature. This factor-complex is divided into a number of component factors. However desirable this may be, since we can gain a knowledge of the effects of the environment only by studying one factor at a time (and attempting to leave the others "constant"), it is virtually impossible to vary one factor without changing the effects (or the magnitude of the effects) of the other factors.† Hence, it is often virtually impossible to say that a particular species occurs in a particular site because of a specific factor. The literature of bryoeology is full of such speciously simple reasoning—and it is indeed almost impossible to avoid it, since with intensive field work the student acquires a certain familiarity with the "behavior" of the various species under varying conditions. Therefore, he is sometimes tempted to oversimplify by attributing the occurrence (or absence) of a species from a particular site to a single factor, which obviously never occurs or operates alone; i.e., a particular species cannot occur at a particular site if one factor is at an optimum, but one or more of the others are at such a level that they make it impossible for the plant to undergo ecesis.

It should be stressed that often one single factor appears to be the decisive one, when all the other factors are at a level reasonably close to the optimum (Liebig's Law). For example, we can find nearly the same combination of environmental factors in rock-pools at many points along the north shore of Lake Superior; yet only at a few do such species as *Riccardia pinguis* occur. An analysis of the situation reveals that aside from chance, there is only one apparent factor that is important here: most rock-pools are not decisively basic and do not show the presence of *Riccardia*; those rock-pools where the seepage is quite basic often show the presence of *Riccardia*. It is implied here—even if not stated—that the *Riccardia* occurs because of the presence of basic conditions, and because all other factors lie within the limits of tolerance of the species.

Previous work, in North America, in which the various environmental factors have been studied critically is extremely limited in scope and often not of a caliber to meet modern standards. Much more work has been done in Europe, e.g., the rather uncritical but pioneer work of Amann (1928); the work of Schade (1917) on the temperature factor; the work of Apinis and Lacis (1935) and of Olsen (1917) on the pH factor; the work of Toda

* Such a treatment seems best, since a classification based on the habitat is, from the point of view of physiology, sound. Since the physiological requirements of the constituent species, in the final analysis, determine the structure of a community, the community is best treated in terms of the physical environment that conditions its composition.

† For instance, the light, temperature, and moisture factors are closely interdigitated, so that it is perhaps better for most purposes to speak of a transpiration factor. A species such as *Odontoschisma denudatum* will occur on a dry log, when there is little direct sunlight (hence when the evaporation rate is low); it can, however, occur under very sunny conditions when the substrate is more moist. Hence, changing one factor often inevitably results in a change in toleration for another factor or factors.

(1918) on the light factor; the excellent study of the humidity factor (Clausen, 1952). Richards (1932) has presented a very useful summary of the autecology of bryophytes. The following essay utilizes all these sources, as well as personal observations.

In discussing the ecology of the species, the following traditional sequence will be retained here, prefaced by a discussion of "toleration."

ECOLOGICAL AMPLITUDE

Before we can discuss the effects of the various factors, we must recognize that toleration of environmental extremes (of one, or of several factors) is a variable from one species to the next.* We therefore find that various species show a very wide discrepancy in the range of conditions under which they can exist (leaving out aberrant occurrences, where the species may undergo ecesis temporarily because of lack of competition).

A few examples will indicate very clearly how related types may show a tremendous difference in toleration. In Minnesota we find that *Scapania degenerii* is restricted in occurrence to a single site: around the periphery of rather highly insolated rock-pools and seepage-moist crevices where the rocks are basic or subbasic, and the pH normally ranges from 5.8-7.0. The species is essentially restricted to low, calcareous, moist, rocky Tundra.

Scapania nemorosa, on the other hand, is nearly ubiquitous, occurring over both acidic and basic rocks, under conditions of intense insolation and conditions of constantly indirect light, under a pH from 4.0 or less to 7.5 or rarely higher. In addition, the species will occur on decaying logs, on rocks in intermittent streams where subject to submersion, on moist loamy soil, on banks and along paths.† A third species, *S. apiculata* occurs only on moist decaying logs where the measured pH is 4.6-5.2. A fourth species, *S. cuspiduligera* occurs only as a pioneer over moist basic rocks, where the pH is approximately 6.7-7.2. We find, therefore, even within one genus, great extremes in toleration of environmental extremes. Of the above species, *S. degenerii* is restricted almost exclusively to regions with an arctic-alpine climate or microclimate; *S. nemorosa* occurs from the subarctic to the subtropics

* The important study by Clausen (1952) has also shown that there may be considerable shifts in tolerance (as of, for example, tolerance to desiccation) within the species. Höfler (1943) has also shown that various forms of *Plagiochila asplenoides* may display extraordinary differences in resistance to desiccation. It is impossible to definitely decide, at present, whether these differences are a consequence of "conditioning" or whether they are due to genetic differences. However, the work of Höfler (1945) and of Clausen (1952) suggests strongly that there is seasonal variation in resistance to desiccation in some species, while other species remain uniform in this respect.

† Southeastward, in the coastal plain, the species becomes limited almost exclusively to the bark of living trees. Presumably shift in toleration, and a difference in genotypes, are involved. It must also be recognized that at the edges of the range of a species the species usually occurs in only a limited number of genotypes. Particularly with those of our species occurring as disjuncts, at their southern or western limits, the regional populations are surely genetically very stenotypic. The impact of population size, and isolation, on the ecological amplitude and toleration of a species is still very poorly known. However, the so-called "rigid" disjuncts of Hultén and the "conservative" species of Fernald, probably represent examples of this phenomenon. The widespread destruction of genotypes during the Pleistocene probably played a role in this.

(in northern Florida). *S. apiculata* occurs strictly in regions where the climate is subarctic; *S. cuspiduligera* again occurs largely in areas with an arctic or high subarctic climate; hence these species show not only variations in the breadth of toleration of edaphic and light conditions, but sharp differences in the breadth of toleration of temperature conditions (and, by implication, in length of growing season, length of time covered by snow, etc.).

As is to be expected, such species as *S. nemorosa* are common and ubiquitous under a wide variety of conditions, while such species as *S. apiculata* and *cuspiduligera* show a highly circumscribed occurrence and are much more rare.

Ecological amplitude of a species is also variable from one region to the next.* Very generally we find that nearest the center of distribution of a species (where normally the factor-complex as a whole is more nearly optimal) the species occurs under a very wide and varied set of conditions and can compete successfully in the most varied habitats. Inversely, at the periphery of the range of the species, it tends to have a much more sharply circumscribed ecological range, being restricted in occurrence to one or two sites. For instance, in northeastern Minnesota such species as *Scapania mucronata* and *Lepidozia reptans* have a very wide ecological distribution, occurring under the most diverse conditions: on humus over moist rocks, on bare rock walls, on decaying logs, etc. As the southern edge of distribution of these species is reached in southern Minnesota, we find them sharply circumscribed in occurrence, inhabiting only limited microenvironments over shaded, moist, sandstone ledges.

In this connection it may also be instructive to cite the occurrence, in France, of *Pellia epiphylla* and *P. fabbroniiana* under sharply discrete conditions. Dopp and Chalaud (1926) found that *P. epiphylla* occurs on acid soils (pH 4.85), and *fabbroniiana* on basic soils (pH 7.3). In central and western New York the writer also observed that the species showed a similar ecological distribution with regard to pH. However, in Minnesota, *P. epiphylla* shows a widely expanded pH range, occurring under acid conditions (as on the acid moor of the bog at Kerrick, with such extreme oxylophites as *Cladopodiella fluitans*), as well as under basic conditions (pH 6.8-7.2) as in the ravine of the Manitou River, where it occurred with *Scapania gymnostomophila*, *Preissia quadrata* and *Gymnostomum*—pronounced basiphytes, as well as in close juxtaposition to *Pellia fabbroniiana*. Although *P. epiphylla* shows this pronounced increase in toleration with respect to the pH factor, we find that in Minnesota at least *P. fabbroniiana* retains its basiphyte nature, occurring only under slightly to distinctly basic conditions.

The most extreme instance known to the writer of variation in tolerance, from one region to another, is exhibited by *Porella pinnata*. As I have pointed out in Part I (p. 551), this species is sharply restricted to moist sites, usually subject to inundation, northwards (and in the few stations in western Europe, where it occurs as a rarity). Southwards the plant becomes ubiquitous in regions with a relatively high humidity, and may occur on the bark of various trees (*Fagus*), or even in festoons on the twigs of *Ilex decidua*, high above the point of possible flooding. It also occurs southwards on relatively dry rocks, or on the faces of exposed cliffs, where it is subject to extremely intermittent moisture condi-

* It should also be emphasized that the ecological amplitude of a species in nature is determined not only by climate and the chemical and physical factors of the habitat, but also by competition with other species. Therefore, the amplitude in occurrence in nature of a species, with regard to any single factor or to all factors, is apt to be narrower than that which would obtain in pure culture with competition eliminated.

tions.* Possibly the explanation for such wide discrepancies in toleration lies in the fact that southward, in the center of abundance, *P. pinnata* is an obviously morphologically (and putatively also physiologically) variable taxon, consisting of a series of diverse genotypes, while northward and in western Europe it occurs only in a limited series of closely allied and similar genotypes.

Associated with shifts in tolerance, the pattern of occurrence of a species may change radically from one region to another. For instance, in central and western New York we find that *Frullania asagrayana* occurs almost exclusively on the bark of trees; to the west, in northeastern Minnesota and eastern Kansas it appears almost confined in occurrence to bare or lichen-inhabited rock-walls. In the Appalachians it occurs on both substrates. Similarly, in the very moist fog-forests of the summits of the Smoky Mountains, in Tennessee and North Carolina, we find a large number of species commonly on bark, such as *Tritomaria exsecta*, *Jamesoniella*, *Anastrophyllum hellerianum*, *Nowellia*, and *Radula obconica*, which occur in Minnesota exclusively on shaded logs or moist rock-walls. As has been pointed out (Schuster, 1949) a change in one factor (humidity and precipitation) may act as the trigger-mechanism in some cases in limiting the occurrence of a species, although genotypic differences in toleration may be responsible in others.

Considering the Hepaticae as a whole, we can, however, generalize and state that the vast majority of species have a narrow and sharply defined occurrence (hence narrow ecological amplitude), compared to the majority of Angiosperms. This narrowly circumscribed occurrence gives the Hepaticae (and mosses as well) a definite value as indicators both of microedaphic conditions and of microclimates. It should be recognized that they often have only a limited value as indicators of macroclimate and macroedaphic conditions. For example, *Bazzania trilobata* is a common species with toleration for only quite acidic conditions. Yet this species is often common in areas where the soil and exposed rock outcrops are all quite basic. The *Bazzania* in such areas is a species of advanced ecological conditions, coming in after the accumulation of an acid peat or humus layer; hence can serve only as an indicator of the pH of the few centimeters of surface materials, while the pH of the underlying soil may be quite alkaline. This explains, frequently, the juxtaposed occurrence of higher plants (with a deeply penetrating root system) that are indicators of basic conditions, and of bryophytes (with a shallowly penetrating rhizoid system) that are indicators of very acid conditions. Richards (1932) and Brinkman (1929) as well as many of the continental European botanists have proposed using bryophytes (especially mosses) as indicators of sites.

ECOLOGICAL FACTORS

THE CLIMATIC FACTORS

Temperature.—In general, the incidence of bryophytes, and especially Hepaticae, is highest in environments with a relatively low amount of temperature variation. Both in cool regions, where the summer temperature is low (as in mountainous areas in otherwise warm or hot areas), as well as in the tropics, where the maximum average summer temperature is less than 60° F greater than the average winter temperature, we find a high incidence both of species and individuals of Hepaticae. In the eastern half of the United States, for instance, the richest hepatic flora is to be found in the mountains of New England and of the Appalachians, where the winter temperature

* This duality in occurrence is also emphasized as typical for the species by McGregor (1955), in eastern Kansas.

is low—but the summer maximum is also low (e.g., with at most a 60-70° fluctuation in temperature annually, in the microenvironment), and in areas immediately adjacent to large bodies of water (which exert an oceanic effect and lessen temperature extremes), such as the Great Lakes area, and peninsular Florida. In contrast, areas with a high temperature fluctuation usually have a very poorly developed hepatic flora.*

This is readily evident even within the area of Minnesota. In the southwestern counties, with a high (70-74°) difference between average July and average January temperatures, fewer than a dozen species of Hepaticae have been found, while in the northeastern area along Lake Superior with a low fluctuation (45° or less), over 120 species have been found.†

In general, therefore, areas with oceanic climate have a richly developed hepatic flora, while areas with extremes in temperature fluctuation (e.g., regions with continental climate), have a less rich and diversified flora.

Temperature as an ecological factor is notoriously difficult to evaluate for several reasons. Firstly, its effect cannot easily be kept isolated from the effects of visible radiation (i.e., light). Secondly, we do not know, in a specific situation, what aspect of the temperature factor is the effective or limiting factor; for example, is absolute maximum or absolute minimum, average daily, yearly average, average maximum during growing season, the limiting factor in the northward and southward distribution of a species? Thirdly, the limiting factor in the distribution of a species appears to be largely a factor of the microenvironment, or microclimate; hence the macroclimate recorded by the meteorologist is of extremely limited use in studying the ecological distribution of such small species of limited niches as the Hepaticae.‡ The work of Schade (1917) with the hepatic *Mylia taylori* and moss *Webera nutans* graphically illustrates this. He buried thermometers in tufts of plants that grew 50 meters apart; yet their average yearly temperature

$$\frac{(\text{maximum} + \text{minimum})}{2}$$

differed by over 17°C. He found, furthermore, that the actual temperature of the moss-mat fluctuated between the temperature of the rock surface and of the air temperature. Significantly, in winter time the temperature of the moss-mat was much higher than that of the surrounding air, and after many days of freezing temperatures unfrozen water droplets still occurred among the moss plants. The very considerable temperature differences, within a very small area, that may obtain in a superficially nearly "uniform" area are very clearly brought out by the work of Clausen (1952). Clausen measured the temperature (and relative humidity) of several microenvironments on a small hill. She found that the temperature on Aug. 3, at a site where *Calypogeia trichomanis* (== probably *C. muelleriana*) occurred was 21°C (humidity never below 70%); where *Lophozia (Isopaches) birenata* occurred it was 33°C (humidity as low as 40%), while in patches of *Cephalozia brysacea* the temperature ran up to 55°C (humidity down to 25%). Thus, in a small area, the actual temperatures to which the species are exposed at a given time may vary up to 34°C, and the humidity about 55%!

The writer, in limited work with the extremely "xerothermophile" hepatic, *Mannia fragrans*, found that individual patches of the plants showed a tem-

* Evans (1924), for example, reports only 24 species from all of Nebraska—this represents less than one-fifth of the species known from Cook Co., Minnesota. Similarly, McGregor (1955) after seven years of collecting in all 105 counties of Kansas was able to find only 68 species of Hepaticae, a little more than half the number known from Cook County, Minnesota.

† It should be emphasized that this discrepancy is due as much or more, to differences in the precipitation-evaporation ratio; hence the amount of rainfall is also a real factor here, and its effect can scarcely be disentangled from the temperature factor.

‡ Therefore the climatic maps (figs. 17-20) must be interpreted with great caution.

perature at the thallus surface of up to 90° F during a warm day (when the air temperature, however, was only 84° F). Inversely, in midwinter, when the air temperature had gone down to -24° F, the temperature at the thallus surface (under snow) was 32° F (a 56° difference!). It is therefore evident that the summer temperature of plants growing in sunny sites may go up far above the air temperature, while the winter temperature is often also much higher than the air temperature.*

The ability of many Hepaticae to undergo ecesis at sites where the temperature is always very low is well known. Locally, perhaps the most extreme cases are the two following: (1) A pure growth of *Scapania undulata*, growing over a vertical rockwall at the northwest edge of Porcupine I., Susie Islands. The plants here occur in the wash of the waves, with the lake temperature reaching scarcely above 38° F in the summer; no direct sunlight hits these mats of plants, therefore the maximum temperature under which the species grows never is much higher than the lake waters. A single measurement (Aug. 1948, 3 P.M.) showed a temperature of 52° F at the surface of the moss-mat. On the southeast-facing ledges of the same island, the air and rock-surface temperatures, at about the same time, varied from 82-86° F. (2) A pure growth of *Diplophyllum taxifolium* var. *macrosticta*, in a small cave-like hole at the base of a vertical low cliff, in dense moist forest on Lucille I. The plants here occurred in constant shade, with a reflected light intensity never in excess of 12 foot candles. Temperature (Aug. 1948, 1 P.M.) at the surface of the thin mats was 46° F; in full sun the air temperature, near the shore of the island was 78° F. These measurements not only demonstrate the great differences that microclimate may make in the nature of the environment, they further clearly show that microclimatic conditions in such areas result in summer temperature conditions that make survival of arctic-alpine species readily possible.

The leafy Hepaticae of our region almost all show a strong tolerance for freezing temperatures. In many cases, it is clear that the snow-cover protects the plants from the full extremes of the winter temperatures. However, snow never covers many of the cliff-inhabiting species, and these occur either frozen into a solid mat, or occur free, exposed to the extremely cold and desiccating winds. It is certain that such species (*Anastrophyllum michauxii*, *A. saxiculus*, *Lophozia longidens*, etc.) exhibit an extreme tolerance for wind-action (and consequent desiccation), as well as low temperatures, *per se*.

We know that some species of Hepaticae can survive actual temperatures of -40° to -50° F without apparent damage. In the case of the xerothermophyte species, such as the *Riccia* sp., and *Mannia fragrans*, such temperature tolerances do not exist. Our *Riccia* species are almost all clearly annual, and dependent on the large, water-disseminated spores for their year-by-year survival; in more austral climates, these same species may be perennial or biennial. With *Anthoceros* and *Phaeoceros* there is a clear correlation between climate and the life-cycle of the organism. For instance, *Phaeoceros*

* McGregor (1955:130) has also noted that this species, as well as the often associated *Reboulia hemisphaerica*, are killed back to the growing tips if the temperature falls rapidly, while if it falls swiftly from above freezing to 20° F or lower even the growing tips die.

laevis and *Anthoceros punctatus* locally "fruit" (i.e., produce their spores) in August-October, and appear to be completely winter-killed.* In the Lower Austral areas (as for instance in northern Mississippi), these same species often develop vegetatively until November-December and produce mature sporophytes the next March-May. A single, rather inconclusive experiment was made with *Mannia fragrans*, in which the turgid thalli were placed in vials, surrounded by dry ice, and taken rapidly down to a temperature of -39° C . Several trials were run, in one instance the plants were returned to the greenhouse immediately after the temperature within the vial (thermometers were placed through a perforated cork in actual contact with the surface of the thalli) dropped to -39° C ; in other cases the plants were kept at -39° C for 12 hours, 24 hours, 3 days and one week. In each trial, the *Mannia* died off completely. This leaves unanswered, of course, such questions as 1) would the species survive if it were gradually exposed to lower and lower temperatures, as is the case in nature; e.g., how much cold-conditioning is there? 2) Would the species survive these temperatures, if the thalli were first partly desiccated? However, the weedy moss, *Bryum argenteum*, growing with the *Mannia* survived these conditions, in each case, and resumed its growth subsequently.

On the other hand, such xerothermophyte species as *Mannia fragrans* (and the closely related European sibling species, *M. dichotoma*) are able to withstand much higher temperatures than do most of the leafy Hepaticae. A single reading, at the thallus surface, in July 1949, of thalli of *M. fragrans* (on a sunny, sandy prairie terrace above the Minnesota River) gave a reading of 109° F . Undoubtedly even higher temperatures are withstood by this species, since the air temperature was not then the maximum recorded. Mattiolo, using the related *M. dichotoma*, could subject dried plants to a temperature of 94° C for up to 30 minutes without killing the plants. The xerothermophyte nature of these species is therefore clearly correlated with great heat tolerance, when the plants are relatively desiccated. In *M. fragrans* the thalli are invariably much shrunken during hot periods (when the precipitation-evaporation ratio is excessively low), and the species is subject to high temperatures only during periods when the cytoplasm of the cell is undoubtedly quite viscous.

By contrast, other Marchantiales which never occur under xerothermophytic conditions have a perceptibly lower heat tolerance. De Vries, for example, could demonstrate experimentally that *Marchantia polymorpha* would survive temperatures of 44.9° C , while at 46.4° C the thalli were killed.

Light.—The effect of light on the species cannot always be easily separated from temperature effects. As is well known, in any given area we find that with increased light intensity, there is often an increase in tem-

* In *P. laevis*, however, glandular marginal, green swellings may be produced and these remain green into late November, when the rest of the thalli have browned and started to disintegrate. These glandular swellings are formed of smaller cells, densely packed with a more viscous protoplasm and with only very small vacuoles. Probably, these glandular swellings persist and live through the winter locally, resulting in a method of vegetative persistence by the species.

perature, and consequent increase in the evaporation rate. We are then scarcely in a position to speak of the light factor, independently of these other factors.* Furthermore, the quality of the light is possibly important, at times at least, as a limiting factor. Some of the high mountain species must be able to tolerate much larger quantities of ultra-violet light than lowland species. Such assumptions, at present, are wholly speculative and need experimental proof.

In that connection, it may be well to stress the fact that we know nothing (except for a few species like *Marchantia polymorpha*), regarding the effect of day-length. Voth and Hamner (1940) have investigated photoperiodism in *M. polymorpha*. They found 1) that plants grown under a long photoperiod (18 hours light per 24-hour cycle) were larger, and had greater dry weight than those grown under a short cycle (9 hours light per 24-hour cycle); 2) plants grown under the long photoperiod produced a larger number of the stalked archegoniophores and antheridiophores, while plants on the shorter cycle produced a larger number of gemmae cups. This is in accord with the tendency of the species, in general, to produce (under greenhouse conditions) very abundant gemmae cups in autumn (as the day length lessens), while the antheridiophores are produced in February-March and the archegoniophores in March-April, or even May.

Although no experimental data are at hand, such phenological differences appear correlated with photoperiodism in many other Hepaticae, and deserve further attention.

It is probable that photoperiodism is not as strict a limiting factor in the distribution of Hepaticae as it is in some higher plants, since so very many of the Hepaticae reproduce exclusively or largely by asexual methods of reproduction. Field observations strongly suggest that, in at least some cases, such asexual reproductive modes are not seasonally limited during the growing season.

The effect of light intensity on a closely related group of species has been studied by Buch (1933). His data, which have many important taxonomic implications, are briefly summarized here since they appear in part also to relate to the photo-period. More critical experiments than his are needed to definitely demonstrate this assumption. Working with species of *Lophozia*, Buch found that:

1. In the fall, with lower light intensity (and shorter day-length), the leaves of *L. longidens* and *ascendens* (= *gracillima*) became smaller and narrow (mod. *parrifolia*);

* The interlocking operation of these factors is well illustrated by the case of the Susie Islands. These islands, running approximately from southwest to northeast, have a shaded, northwest-facing side, and a sunny, southeast-facing side. The cliffs at the edges, near the water, are very similar on both sides of the islands, yet the cryptogamic flora is vastly different. On the southeast-facing sides, we usually find a dearth of Hepaticae, though some mosses (such as *Hedwigia* and *Grimmia*) and a variety of lichens are common; rarely *Cephalozia* and other xerophytic Hepaticae occur. In contrast, the northwest-facing side is densely colonized by many moss communities, and over 70 species of Hepaticae have been found on this exposure. Although one is tempted to say that the lesser light intensity of the northwest side of the islands "results" in a more favorable environment for hepaticas, it must be recognized that the lesser light intensity there is associated with lower temperatures and a lesser evaporation rate, e.g., the saturation deficit there is at all times much less.

the same was observed in the other species studied (*L. silvicola*, *ventricosa*, *porphyroleuca*).

2. *L. porphyroleuca* differs physiologically from the very similar *L. ventricosa* (and *silvicola*). Forms of *L. porphyroleuca* grown under intense light produce phenocopies almost indistinguishable from forms grown in weak light (mod. *parvifolia*) of *L. ventricosa*. In the diffuse light of late fall, *L. porphyroleuca* ceases growth entirely, while the other species continue to grow, as the mod. *parvifolia*. Buch concludes that the higher light requirements of *L. porphyroleuca* are apparently also correlated with a higher light- and heat-resistance.

3. *L. longiflora* is possibly only a robust, red-pigmented modification (mod. *colorata*) of *L. wenzelii*; i.e., it is a "form" produced by greater light intensity, and not a distinct species.

The data regarding *L. porphyroleuca* and *ventricosa* are particularly instructive, since they corroborate some of the assumptions which have been made regarding various Hepaticae, to the effect that the physiological difference between these species is often very considerable—and greater than the morphological differences in extent. The experiments of Buch should be repeated to show whether diminishing light intensity, or a shorter day-length is responsible for the cessation of growth in fall of *L. porphyroleuca*.

The effect of light as a limiting factor in governing the distribution of species in nature is problematical. However, it is very probable that the exclusion of many species from areas with a very high light intensity (such as sunny cliffs) is due more to the inability of these species to undergo ecesis under conditions of a very high saturation deficit, rather than inability of these species to tolerate high light intensity *per se*. There are very few Hepaticae that appear to be obligatory "sciaphiles" (shade-loving); among them are presumed to be such species as *Cyathodium cavernarum*, and the moss *Schistostega osmundacea*. But in the former case such restriction to deeply shaded areas is assumed, not demonstrated. In most cases, light as such appears to play a relatively small role in limiting the distribution of Hepaticae.

This is abundantly clear when we study the composition of such pioneer communities as the *Lophozia bicrenata*-*Cephaloziella rubella* Associae of rather open Oak-Hickory forests, or of dry soil over ledges, etc. This community, occurring in strongly insolated areas at all times, consists of species characterized under such conditions by thick-walled leaf-cells (a modification for lessening the evaporation-rate) which are reddish to reddish-brown pigmented (a modification apparently for cutting down the intake of light of certain wave-lengths).

It is often the case that a species which is green in shaded situations, develops "protective" pigments in sunny sites. Many, if not most species have the ability to develop such a protective mechanism. The ability of such pronounced light-tolerating species as *Ptilidium ciliare*, *P. pulcherrimum*, *Scapania nemorosa*, *Lophozia silvicola*, *L. ventricosa*, *L. excisa*, *L. bicrenata*, *Frullania eboracensis*, *F. asagrayana*, etc., to develop reddish-brown to purplish pigmentation is well known.* Strikingly, related species often lack this ability altogether. For instance, *Scapania apiculata* and *Lophozia longidens* appear to nearly lack the ability to develop any type of brownish pigmentation of the leaves.

* See in this connection, e.g., de Virville (1934), and in particular the important study of Müller (1916), in which the adaptation of Hepaticae to high light intensity is discussed.

In other cases, we find that various parts of the plant react differently to increased "doses" of sunlight. For instance, *Scapania irrigua*, under all conditions, retains greenish gemmae (i.e., their walls do not develop pigmentation), while the related *S. paludicola* develops brownish gemmae even under shaded conditions, when the rest of the plant is green and devoid of secondary pigments.* Under conditions of strong insolation, the cell-walls of *S. paludicola* become brownish to reddish-brown, like those of the gemmae. However, in *S. gymnostomophila*, where the gemmae are also reddish-brown in diffuse light, increased sunlight has little effect; the plant retains its green to blackish-green color, while the gemmae are similarly reddish-brown as in shaded sites. For the taxonomist, an understanding of the reaction-pattern of the various species to different light conditions is of paramount importance in order that the most difficult species complexes (such as *Lophozia* and *Scapania*) be properly understood.

In general, it is probably correct to state that the Hepaticae are more shade-tolerant than most mosses and less light-tolerant. For that reason, under conditions of intense insolation, the cryptogamic flora usually consists nearly entirely of mosses (and lichens), while with conditions of greater shade, a larger proportion of Hepaticae play an important role. This is by no means always the case, however, as is illustrated by observations (Thatcher, 1950) in a cave at Crystal Springs, Wisconsin. Surrounding electric light bulbs in this cave were a rather large number of species of mosses (*Funaria hygrometrica*, etc.) but only the single, extremely tolerant hepatic, *Marchantia polymorpha*.†

It may be instructive to list some of our species as to light toleration. A very few species occur so normally in full sun (or nearly full sun) that they must be considered light tolerant; others occur so constantly in dense shade, they must be considered shade tolerant (and perhaps light-intolerant, although this is very difficult to prove). Perhaps the largest number of species are clearly tolerant of both shade and light conditions, if moisture conditions are sufficiently close to the optimum. For that reason, a grouping into three categories appears desirable:

Light-tolerant "Photophile"

<i>Ptilidium ciliare</i> *	<i>R. trichocarpa</i> *	<i>Preissia quadrata</i> *
<i>Cephaloziella rubella</i> *	<i>R. austini</i> **	<i>Reboulia hemisphaerica</i> *
<i>Cephalozia ambigua</i>	<i>R. dictyospora</i> *	<i>Phaeoceros laevis</i>
<i>C. bicuspidata</i>	<i>R. hirta</i> *	<i>Notothylas orbicularis</i>
<i>Lophozia capitata</i>	<i>R. sorocarpa</i> *	<i>Mylia anomala</i>
<i>Odontoschisma denudatum</i>	<i>Ricciocarpus natans</i>	<i>Gymnocolea inflata</i> *
<i>Lophozia birenata</i> *	<i>Mannia fragrans</i> *	<i>Cephaloziella byssacea</i> *
<i>Riccia fluitans</i>	<i>Cephaloziella subdentata</i> *	

* Based upon field observations of over one decade. These fully confirm the experimental data of Buch (1928).

† As is evident, all of the mosses listed in that paper, as well as the hepatic, grow well in areas with intense sunlight. They are therefore facultative shade-plants. This is not true of a few cave-bryophytes, such as *Schistostega osmundacea*, which appear to be obligatory shade plants. In the latter species, strong light intensity proved to have a lethal effect, even when the evaporation-rate was kept low. Two separate workers found that the minimum average light intensity under which the moss could exist was 1/500, though Lundegardh (Svensk Bot. Tidskr. 15:78, 1921) found that it grew well with a *maximum* light intensity of 1/650.

Tolerating both light and shade

<i>Nowellia curvifolia</i>	<i>Marchantia polymorpha</i>	<i>F. eboracensis</i>
<i>Bazzania trilobata</i>	<i>Conocephalum conicum</i>	<i>F. asagrayana</i>
<i>Blepharostoma trichophyllum</i>	<i>Lophocolea heterophylla</i>	<i>Solenostoma pumillum</i>
<i>Jamesoniella autumnalis</i>	<i>Riccardia pinguis</i>	<i>Scapania curta</i>
<i>Scapania mucronata</i>	<i>Calypogeia sphagnicola</i>	<i>Lepidozia reptans</i>
<i>S. undulata</i>	<i>Anastrophyllum minutum</i>	<i>Ptilidium pulcherrimum</i>
<i>S. nemorosa</i>	<i>A. michauxii</i>	<i>Blasia pusilla</i>
<i>Lophozia alpestris</i>	<i>Diplophyllum apiculatum</i>	<i>Cololejeunea biddlecomiae</i>
<i>L. excisa</i>	<i>Pellia epiphylla</i>	
<i>L. porphyroleuca</i>	<i>Cephalozia lichenoides</i>	
<i>L. kunzeana</i>	<i>Frullania bolanderi</i>	

Shade-tolerant "Sciaphile"

<i>Diplophyllum taxifolium</i>	<i>S. glaucocephala</i>	<i>Geocalyx graveolans</i>
<i>Lophozia longidens</i>	<i>Riccardia multifida</i>	<i>Metzgeria conjugata</i>
<i>Cephalozia media</i>	<i>R. palmata</i>	<i>Pellia fabroniana</i>
<i>C. connivens</i>	<i>Calypogeia suecica</i>	<i>Moerckia hibernica</i>
<i>C. macounii</i>	<i>C. trichomanis</i>	<i>Mannia rupestris</i>
<i>C. lacinulata</i>	<i>C. meylanii</i>	
<i>Scapania apiculata</i>	<i>Anastrophyllum hellerianum</i>	

If the above table is inspected, it will be seen that the Marchantiales belong overwhelmingly to the group that is light-tolerant (or tolerant to both light and shade), only *Mannia rupestris* being largely a shade plant. This group is characterized by morphological adaptations to extreme light and high evaporation rate; it includes largely xerophytes (asterisk). The gametophyte is highly differentiated in such plants, often with large purplish ventral scales, and has the chlorophyllose tissue protected by an epidermal layer provided with pores; such plants are further characterized by their reduced sporophytes.

On the other hand, the shade-tolerant types (or obligatory shade-plants) are all leafy forms (Jungermanniales) or delicate thallose types (Metzgeriales), except for the *Mannia rupestris*. These plants are characterized by a lack of morphological specialization to resist a high evaporation rate, and have delicate, long-stalked, ephemeral sporangia.

Another generalization that may be made is that the annual types (*Riccia*, *Anthoceros*, *Notothylas*) and the types that die down except for the shoot-apices (*Blasia*) are all either light-tolerant, or tolerate both light and shade. In contrast, all the pronounced shade-types are perennial plants. A further generalization is that the light-loving types quite generally lack specialized asexual means of reproduction (gemmae, caducous leaves, etc), while the tolerant or shade-loving types very predominantly develop some means of asexual reproduction.

A final generalization important to note is that all of the light-tolerant types listed above (except the Anthoceratales, *Riccia fluitans* and *austini*) are able to develop reddish-brown to purplish pigmentation. By contrast, of the species in column 3 (shade-loving or tolerating types) only *Diplophyllum taxifolium* and (to a slight degree) *Riccardia palmata* are able to develop secondary pigmentation. It is, therefore, perhaps pointless to stress that one can logically conclude that the light-tolerating species are able to undergo ecesis under strongly isolated conditions because they have mechanisms to cut out injurious quantities of light, while the shade-loving species are unable to invade such sites, since they largely lack any ability to develop secondary

protective pigments. This is certainly not the entire story, but it appears to be one of the real limiting factors in the distribution of species as regards the insolation of the habitat.

The ability of some of our species to undergo ecesis in areas with a very low light intensity is also emphasized by some published figures (which, however, unfortunately do not state whether reflected or incident light is measured).

Plagiochila asplenoides, growing in deciduous forests, may exist under a light intensity of 1/2-1/10 (in March-May, before the leaves develop), while in the deep shade of beech forests it will grow at a light intensity of only 1/50-1/60 after the leaf-canopy develops. Similar great seasonal fluctuations exist for many of the species common to deciduous forests, while in the cold boreal forests, seasonal fluctuation of this type is less extreme. A tempering factor, often overlooked, is the lessening of light intensity (normal daylight), and its daily duration, during the winter months, when the leaf-canopy does not intercept most of the incident light, compared with the summer.

Many cave bryophytes have been studied, and light readings made. The following represents a compilation of the more widely known cases:

<i>Calyptogeia neesiana</i>	1/330
<i>Conocephalum conicum</i>	1/50, 1/371, 1/400
<i>Pedinophyllum</i>	1/50, 1/180, 1/300
<i>Porella platyphylla</i>	1/36
<i>Lejeunea canifolia</i>	1/300

Under the more extreme conditions cited above, however, the development of the species is hardly normal, usually a modification *parvifolia-laxifolia-viridis-leptoderma* resulting (as regards the leafy species).

A single species of Hepaticae is known which habitually grows entirely without light—the gametophyte growing several inches below the surface, under moss-mats. This species, *Cryptothallus mirabilis*, belonging to the Ricciaceae (Aneuraceae), however, exists as an obligate symbiont with a fungus, which synthesizes all of the food utilized by the *Cryptothallus*. This latter genus, though at present not known outside of Europe, will probably be found eventually in our coniferous forests.

Moisture.—As has been previously stated, increased light intensity (and associated increases in temperature) are associated with a higher evaporation rate, thus higher saturation deficit. For that reason, and others, it is often virtually impossible to keep consideration of the moisture factor free from the temperature and light factors.

Although all of the bryophytes fall arbitrarily into two groups, aquatic and terrestrial types, physiologically they are all presumed to be poikilohydrous (Walter, 1931, p. 9). There is also a very large group of intermediate types of bogs and swamps (hygrophytes, or "helophytes"). The former grouping is partially artificial, since there are few aquatic Hepaticae (*Chiloscyphus* spp., *Scapania undulata*, *Ricciocarpus natans*, *Riccia fluitans*), all of which also have terrestrial "phases." Only *Riella* is predominantly aquatic; this, however, also produces subterrestrial phases. Tolerance towards varied moisture conditions shifts radically in some species, as one goes from a large geographical area to the next. For instance, *Porella pinnata* in Europe is a pro-

nounced hygrophyte, usually occurring over stones in brooks; this is also the case in the more northern portions of North America (New York west to Minnesota). However, in the southeastern states the species may occur under extremely xeric conditions on bark of beech, 6-8 ft. above the highest point to which water reaches, or over dry cliffs (with *Frullania squarrosa* and *tamarisci*, *Asplenium trichomanis* and *platyneuron*) which are moist only when rains occur (as in West Virginia to Kansas and to Mississippi). Why the species should show this variation in moisture-requirements is difficult to explain. Perhaps, in the southeastern states (where it is very abundant and the dominant species of the genus) the species occurs under optimal temperature conditions, and there can "tolerate" a wider range in moisture conditions *vs.* a less optimal occurrence further northward, associated with a very narrow range of moisture conditions. More probably (as is suggested elsewhere) such phenomena are associated with genetic differences of a species from one region to another.

Similar cases showing a "shift" in occurrence have been cited (Schuster, 1949, pp. 131-132). Of these, *Radula obconica*, *Anastrophyllum michauxii* and *Tritomaria exsecta* are among the most interesting. These species, occurring locally almost entirely over moist rock-faces (the *Tritomaria* and *Anastrophyllum* also on logs), are found in the humid, temperate rain-forest conditions that obtain in the southern Appalachian Mountains, commonly on bark, often 6-8 ft. above ground level. In this case, the limiting factor in the ecological distribution of the species clearly appears to be the frequency of fog and the saturation-deficit of the air; the species appear to be equally intolerant of a high saturation-deficit everywhere throughout their range. On the other hand, *Cololejeunea biddlecomiae* appears to become more tolerant of low atmospheric humidity, and of desiccation, from north to south.

Of the few species with truly aquatic phases, most belong to the benthos (i.e., are attached), such as *Porella pinnata* and *Chiloscyphus* spp. However, two of our species are regularly planktonic (*Riccia fluitans*, *Ricciocarpus natans*), while a third, helophytic species, *Cladopodiella fluitans*, often forms floating mats in pockets of water in bog-holes. These species, however, all have terrestrial phases, and mostly grow in areas where the water-level fluctuates strongly, resulting in occurrence of alternating aquatic and terrestrial phases.

The terrestrial species, which are in the very vast majority, usually appear more restricted to areas with high atmospheric moisture (and are therefore more sensitive to the saturation deficit) than the higher plants.* This is correlated in part with the absence of roots in the bryophytes, but very largely appears due to the greater over-all delicacy, and especially the very large surface-area, compared with their tiny bulk. This is especially the case with the leafy forms with patent leaves. K. Müller (1909) states that some species are able to absorb water from a saturated atmosphere and can hold

* It has not been generally recognized that even the corticolous, xerophytic types of Hepaticae occur in niches with a relatively high humidity. Thus Clausen (1952, p. 36) showed that "on an extremely hot day after a prolonged period of drought" when the corticoles were exposed to the lowest humidity "to which the plants are exposed during the year . . . they (i.e., the humidities) are still not remarkably low." *Frullania* spp. and *Metzgeria furcata* were found to grow under a humidity, at such times, of 55-62% and 68%, respectively.

such water by capillarity.* This ability of species to absorb atmospheric water is probably correlated with the wide distribution of epiphytic types in areas of high rainfall and high-fog incidence (such as the southern Appalachian Mountains), and their relative rarity locally (where rainfall averages only ca. 25 in. for the state as a whole, and where fog is rare or infrequent).† For that reason, as well as for others, some families (Radulaceae, Frullaniaceae, but especially the Lejeuneaceae) are very poorly represented locally, while other largely epiphytic genera (such as *Metzgeria*) are absent or very rare.

Since, in general, Hepaticae are plants of moist environments, the relatively arid prairie regions are nearly free of them. Notable local exceptions are *Mannia fragrans*, a species with a thick dorsal epidermis with thick-walled cells and with very large, deep-purple ventral scales, and some species of *Riccia*, such as *R. austini*. The edges of the thalli curl up as the plants dry, in these species, the dorsal epidermis gradually becoming almost hidden while the imbricate ventral scales become exposed and connivent towards each other dorsally. A similar case, perhaps less extreme, is *Mannia sibirica*, which often occurs adjacent to the goat-prairies. It also curls up during periods of drought, the very strongly imbricate, deeply purplish-pigmented ventral scales becoming prominent (and then showing a characteristic, metallic sheen). These species very evidently are able to survive several weeks of drought at a time.‡

It is also probably a valid generalization to state that most of the Jungermanniales (leafy Hepaticae) show rather pronounced "physiological" drought

* The importance of absorption of water from the air appears to be much less important than assumed at one time. Anderson and Bourdeau (1955), working with two mosses, *Atrichum angustatum* and *Polytrichum commune* found that non-turgid plants failed to regain turgor after 5 weeks storage at 100% relative humidity. Furthermore, turgid plants, of both species, kept for 5 weeks at a relative humidity of 95% showed "wilting" and in the *Atrichum* even those plants kept at 100% relative humidity lost turgor. Patterson (1943), working with a series of mosses and hepaticas ranging from hydric to xeric, found that the "variations in amount of moisture absorbed at various humidities are minor ones," and that "there is no consistent difference between the absorptive capacity of the ecologically diverse bryophytes tested. Thus there appears to be little or no correlation between the degree of xerophytism of the bryophytes investigated and their absorption of atmospheric moisture."

† It should also be pointed out that the Hepaticae occurring on bark are, by and large, far more sensitive to desiccation than mosses and lichens. Pessin (1925), for example, found that lichens showed the greatest tolerance of desiccation, the associated corticolous mosses (*Orthotrichum*, *Leucodon*) less tolerance, and the associated hepatic (*Frullania eboracensis*) showed the least tolerance.

It is also evident that certain corticolous communities are "fog forest communities" even in temperate zones. In the Southern Appalachians, at elevations of over 5000 feet, a community of *Metzgeria fruticulosa*-*Microlejeunea ulicina*-*Frullania oakesiana*-*Ulota crispa* occurs, closely associated with the fog-shrouded summits of the highest peaks. Amann (1928, p. 60) ascribes a similar association of *M. fruticulosa*, *M. ulicina* and *Ulota* and the alga *Trentepohlia abietina* (which is also found associated in the Appalachians) to montane areas of Switzerland with at least 20 days of fog per year, but becoming common in areas with more than 50 days of fog annually. I am convinced that such "sociétés de mousses néphélophiles" are actually restricted to areas where moisture occurs in the air in the form of actual droplets (i.e., liquid, rather than atmospheric water) during many days per year.

‡ The most extreme example of drought-resistance known to me is that of *Riccia atrovirginata*. Material of this species was sent to me by Dr. Eula Whitehouse from Texas.

resistance. By this we mean that the various species show no direct mechanism by which water-loss can be reduced, yet the species are able to survive rather prolonged periods without water. Such generally xerophytic species as *Lophocolea minor* and occasionally xerophytic species as *Plagiochila asplenoides*,* fall into this category. In other cases, we find direct "mechanical adaptations" for either holding capillary water or for absorbing it rapidly (or both). Among such adaptations are to be classed the capillary divisions of the leaves of *Ptilidium*, a genus with pronounced toleration for xeric environments; the closely imbricated leaves of *Anthelia juratzkana*, and of such extra-territorial genera as *Temnoma* and *Gymnomitrium*; the thick-walled, strongly collenchymatous cells of *Odontoschisma macounii*, of *Ptilidium*, etc.; the strongly verruculose cuticle of *Cephalozia subdentata* and *bryosacea* var. *scabra*; the "water-sacs" formed by the ventral lobes, or lobules, of *Radula* and *Frullania*, and the various *Lejeuneaceae*.

The interpretation of such "adaptations" as effective in promoting water uptake (and/or inhibiting water loss) has been criticized (Herzog, 1926, pp. 58-59). Herzog is of the opinion that only morphological adaptations which reduce the exposed surface area of the plant are effective in diminishing water-loss. It is certainly true that "physiological" resistance is probably much more effective in Hepaticae, particularly in the leafy species, than "structural adaptation," in allowing their survival in areas with intermittently "adequate" moisture. This opinion is shared by Walter (1931, p. 18), and appears to be reinforced by the experiments of Höfler (1942, 1943, 1945, 1950) who has made many experiments, on a number of species, and found that the ability to withstand desiccation varies greatly from one species to the next. Höfler also demonstrated that there was a connection between habitat and degree of resistance to desiccation. Finally, Clausen (1952) showed experimentally that the ability to retain turgor, after a rain, is correlated only to a limited degree with the presence of structural features that have been considered to be "xeromorphic adaptations." The most effective factors slowing down loss of turgor appeared to be shoot size (the larger the shoot, the slower loss of turgor), and the development of capillary spaces, allowing the retention of water.† She concluded that it was impossible to demonstrate any clear connection between the distribution of species in nature, and their ability to retain water, and "consequently the morphological and anatomical characters are of little ecological value."

On the other hand, the thallose Metzgeriales in general show no modifications for drought resistance and (except for *Pellia*, which rarely develops

It was moistened, placed in a petri dish, one year and 3 months after being "packetized" and dried, and showed clear evidence of growth within 5 days after being moistened. The plants were then placed in the greenhouse where they were successfully grown for nearly a year. Similar drought resistance is not known for other Hepaticae, in the vegetative state, but has been reported for such mosses as *Tortella inclinata* and *Grimmia pulvinata* (see discussion by Richards in Verdoorn, 1932).

* The pronounced variation in resistance to desiccation of this species is dealt with on page 232.

† See, however, the paper by Blomquist (1929), in which it is shown that the capillary spaces, formed by the "water sacs" of the leaves of *Frullania* are unable to "hold" water for any considerable period after the surface of the plants begins to dry.

reddish pigmentation) show little or no ability to develop secondary pigments. In general, the members of this order, correlated with slight morphological adaptation towards intermittent moisture conditions, are very strongly limited in their occurrence by the moisture factor; all are usually mesophytes or hygrophytes.*

The thallose Marchantiiales, however, show a definite morphological adaptation for strongly intermittent moisture conditions, and are usually even more tolerant to such conditions than the Jungermanniales. This is readily evident when we compare the predominantly Marchantiaceous hepatic flora of the southeastern corner of Minnesota (with its less favorable P/E ratio), with the very slight Marchantiaceous element in the flora of the northeastern corner of the state (with its favorable P/E ratio).

In this connection, it should be stressed that the amount of moisture available to the various species, and the constancy with which this moisture is available are not only a function of the rainfall (which we can find from the meteorological records), but very largely also of the evaporation rate. The latter, in turn, is directly a factor of wind velocity, insolation and temperature, and to some degree of other factors. Therefore, it is more reasonable to study the distribution of the various species using the saturation-deficit, or the precipitation/evaporation ratio. These latter indices, measured at the actual niche where the plants occur, will give us a true picture of the moisture requirements of the species. Unfortunately, no meaningful data of this type are available to us at present.

It has been customary to divide plants into three types of terrestrial groups, depending on the amount of moisture available to them, as follows: xerophytes (adapted to dry conditions); mesophytes (adapted to moist conditions; not decided xerophytes or hygrophytes); hygrophytes (adapted to sites where the substrate is virtually constantly saturated with water). In addition, of course, there is the fourth group of hydrophytes, or aquatic plants. It may be instructive to list a few typical Hepaticae belonging to each of these groups:**

Xerophytes		
<i>Lophozia birenata</i>	<i>Lophozia porphyroleuca</i>	<i>Cephaloziella subdentata</i>
<i>Ptilidium ciliare</i>	<i>Odontoschisma denudatum</i>	<i>C. byssacea</i>
<i>Frullania eboracensis</i>	<i>Gymnocolea inflata</i>	<i>Lophozia kunzeana</i>
<i>F. brittoniae</i>	<i>Mannia fragrans</i>	<i>Bazzania trilobata</i>
<i>F. riparia</i>	<i>M. sibirica</i>	<i>Metzgeria furcata</i>
<i>Porella platyphylla</i>	<i>Reboulia hemisphaerica</i>	

* The humidity measurements of Clausen (1952, p. 31) on *Fossumbronia* are very revealing. She found that in a *Myrica* bog "in warm and bright weather" the relative humidity "decreases greatly upwards in the very lowest layers of air" and may, in the summer, become rather low, "but the sand and the thin layers of humus on which *Fossumbronia* was growing, do not succeed in drying up." Within 1 mm of the ground level, relative humidity was over 90%; at the 5 mm level above ground it had dropped to about 75%, and at the 15 mm level was ca. 70%. In other words, during a period when the macroenvironment was in a state of drought, the microenvironment to which the Metzgerine genus *Fossumbronia* was exposed was damp; the stratum of air immediately surrounding it had a humidity in excess of 90%.

** It must be kept in mind that a species may be a hygrophyte locally (as is the case with the *Porella pinnata* quoted above) while it may become a very pronounced xerophyte elsewhere.

<i>Mesophytes</i>		
<i>Trichocolea tomentella</i>	<i>Lophozia ventricosa</i>	<i>Preissia quadrata</i>
<i>Blepharostoma trichophyllum</i>	<i>Gymnocolea inflata</i>	<i>Phaeoceros laevis</i>
<i>Lepidozia reptans</i>	<i>Metzgeria conjugata</i>	<i>Anthoceros macounii</i>
<i>Calypogeia meylanii</i>	<i>Pellia epiphylla</i>	<i>Fossombronia foveolata</i>
<i>Scapania undulata</i>	<i>Blasia pusilla</i>	<i>Lophozia kunzeana</i>
<i>S. nemorosa</i>	<i>Asterella ludwigii</i>	<i>Bazzania trilobata</i>
<i>S. apiculata</i>	<i>Mannia rupestris</i>	
<i>Hygrophytes</i>		
<i>Porella pinnata</i>	<i>Cephalozia pleniceps</i>	<i>Gymnocolea inflata</i>
<i>Scapania irrigua</i>	<i>macrantha</i>	<i>Scapania nemorosa</i>
<i>S. paludicola</i>	<i>Calypogeia meylanii</i>	<i>S. undulata</i>
<i>Moerckia hibernica</i>	<i>Mylia anomala</i>	<i>Cephalozilla elachista</i>
<i>Cladopodiella fluitans</i>	<i>Lophozia marchica</i>	<i>Lophozia kunzeana</i>
<i>Hydrophytes</i>		
<i>Chiloscyphus spp.</i>	<i>Riccia fluitans</i>	<i>Cladopodiella fluitans</i>
<i>Ricciocarpus natans</i>	<i>Scapania undulata</i>	

It will be seen from the above table that some species (*Scapania undulata*, *Lophozia kunzeana*, *Scapania nemorosa*, *Bazzania trilobata*) occur in two or three of the categories. These species are mostly abundant in their normal range, since they possess a wide amplitude of toleration, both for moisture as well as light conditions. Other species (such as *Ptilidium ciliare*) are listed for one category only, but rarely occur under very different conditions (as in bog-holes, in the case of *P. ciliare*, for instance).

In general, the majority of our species are mesophytes, with the next largest group the hygrophytes, while pronounced xerophytes and hydrophytes are both considerably rarer.

Finally, some of the effects of submersion of terrestrial species in water may be noted. As is well-known, a rather large number of normally terrestrial Hepaticae produce aquatic modifications. In general, if such modifications occur in lentic (slowly moving or standing) waters, the plants become larger, with larger, lax, distant leaves, and usually with larger cells than in the terrestrial parent form. In contrast, if the aquatic modifications occur in lotic (rapidly running, distributed) waters, the plants are usually smaller, with smaller leaves, and usually with smaller leaf-cells (as in the case with the aquatic modifications of *Chiloscyphus pallescens* and *polyanthus*). In most cases submersion is shallow, usually less than 30 cm. However, a few notable exceptions occur, and *Solenostoma riparium* has been noted at a depth of several meters in a lake, while the aquatic modification of *Calypogeia sphagnicola* (fo. *submersa*) may occur in 3 meters of water. Such depths are much less than those noted for various mosses (*Fontinalis*, *Drepanocladus*, etc.) where a maximum depth of over 19 meters has been noted. It is well known that with submersion, the production of sporophytes comes totally or almost completely to a halt. In most cases, indeed, archegonia and antheridia are not produced. When sporophytes are produced, it appears always to be the result of fertilization during a period of low water.

Cognizance should also be taken of the rather pronounced effects that changes in moisture conditions produce on the physical characters of most species. The Marchantiales, under saturated moisture conditions, produce forms in which the air-chambers and pores may be nearly or quite suppressed. In the leafy Hepaticae growth under saturated conditions results, almost

inevitably, in the production of extremely long internodes (and a consequent mod. *laxifolia*), and the production of very delicate cell-walls (mod. *leptoderma*). In many species with normally dentate leaf-margins, such an environment leads to the production of entire-leaved forms (mod. *integrifolia*). Buch, in his experimental work on *Scapania* and *Lophozia* has particularly elucidated the reactions that the species undergoes with changes in moisture conditions. In *Lophozia* he found (1933) that under normally moist conditions (atmosphere not saturated), two species grow suberect (*L. ascendens*, *L. longidens*), while the others (*L. porphyroleuca*, *L. ventricosa*, *L. sylvicola*, *L. wenzelii*) grow appressed closely to the substrate. However, with a saturated atmosphere, the latter group of species (and virtually all other Jungermanniinae) also develop an erect type of growth.

In all species with a normally collenchymatous areolation of the leaves, plants grown under unusually moist conditions show leptodermous, thin-walled, delicate cells (mod. *leptoderma*). Some species that occur normally under hygric conditions, such as *Porella pinnata* are characterized by such thin-walled cells. However, under exceptional conditions, when growing on dry bark in sunny places (with an extremely high saturation deficit and high evaporation rate) even this species may produce strongly collenchymatous cells. Buch, in his work with *Lophozia*, found that *L. ascendens* and *L. longidens*, under greatly increased saturation-deficit did not produce very strongly bulging trigones; these species also showed the ability to dry out rapidly, in fact, as soon as the leaf-surface became dry (much as in *Ptilidium ciliare*). They were further characterized by the ability to withstand such rapid and frequent drying out. The other species studied (*L. ventricosa* and *L. porphyroleuca*) produced, under conditions of high saturation-deficit, modifications (mod. *pachyderma*) with strongly bulging trigones; these species also showed a tendency for the leaves to retain their form and turgidity with drying. With decreased moisture, the internodes of the stem also became much shorter (mod. *densifolia*). With greatly decreased moisture content, *L. ventricosa* also produces a mod. *pachyderma-parvifolia* which produces concave leaves, and so closely approaches *L. wenzelii* (in which such a leaf-form is normal, except in extreme leptodermous, lax-leaved forms) that it must be regarded as a phenocopy of the latter. These species are all characterized by the ability to produce gemmae. However, with extreme high saturation-deficit, gemmae-formation is inhibited. *L. porphyroleuca* then becomes completely gemmae-free (= *L. guttulata* of authors).

The great variation in physical form of the species with changed moisture conditions must be recognized as one of the big obstacles to acquiring a clear concept of the species, especially in such difficult groups as *Lophozia* and *Scapania*, where phenocopies by one species, of another, are all too frequent. Some knowledge of the ecology of these species is thus necessary for a clear understanding of their taxonomy.

In addition to the pronounced effect that change in moisture conditions have on the form of the species, there remain to be considered the physiological differences between the various species regarding the manner in which they absorb water. Buch, on this basis, has divided the bryophytes into three groups: the endohydre, mixohydre, and ektohydre. The first group

includes chiefly Marchantiales, few leafy hepatics; in these the rhizoids are supposedly able to absorb water (and mineral materials). The last group includes species which absorb water (and mineral materials) directly through the assimilating leaf-surfaces. The second group (mixohydre) is able to absorb water in both ways. Extreme examples of the ektohydre type are such species as some Lejeuneaceae, that can supposedly absorb water from saturated air (Müller, 1909).* In general, the leafy Hepaticae are all ektohydre. Associated with this, we find that they can generally undergo repeated drying for short periods, and exist under extremely intermittent moisture conditions. Höfler (1943) has shown that some of the ektohydre types, such as *Cololejeunea calcarea* (a sibling species of our *C. biddlecomiae*) and *Porella platyphylla* can be completely air-dried, and will survive such drying for a month or longer. *Ptilidium pulcherrimum*, on the other hand, can stand only a lesser duration of drying.† Some species, however, that are restricted in nature to areas where there is a nearly constantly high moisture will die even with a comparatively slight lowering of the relative humidity. Among such species are *Calypogeia neesiana*, *Solenostoma sphaerocarpum*, *Pellia neesiana*, *Chiloscyphus polyanthus* var. *rivularis*. In the case of *Pellia fabbroniiana* and *Lophozia incisa*—constantly mesophytic species—the plants (fide Müller, 1951) will die even when kept in a relative humidity of 96%.‡

Höfler (1943) has also called attention to the fact that the same species may show differences in its ability to tolerate desiccation. In the large form of *Plagiochila asplenoides* ("var. *major*") the threshold lies at 70% relative humidity, and the plant will not survive levels below this. On the other hand, the small, relatively xeromorphic *P. asplenoides* var. *minor* will survive down to 15-20% relative humidity. To what degree these data indicate we deal with physiological races or ecotypes, is not yet clear. However, the work of the physiologist and ecologist may eventually show that there was some basis for the point of view of such workers as Schiffner, who recognized many varieties and forms under most polymorphic species. Herzog and Höfler (1944) have demonstrated that *Porella platyphylla* shows as high a tolerance for desiccation when plants from very moist sites are tested as when plants from the normally xeric habitats of this species are tested.

This variability, from one species to the next, as regards tolerance to desiccation, is abundantly documented in the study of Clausen (1952). She found that there is variation from an extreme such as *Cephalozia media* (which will die after the plants remain for a few hours in air at a relative humidity of 92%) to *Porella platyphylla* (which will readily tolerate desiccation for over 24 hours at a relative humidity of 0%). She lists, in approximate sequence, the following investigated individual populations of a number of species, showing increasing greater resistance to drought: *Cephalozia*

* Recent experimental work does not support this supposition.

† This experimental work clearly shows its parallel in nature, where *C. biddlecomiae* and *P. platyphylla* are members of the relatively xeric corticolous *Frullania-Radula-Lejeunea* community, while *Ptilidium* is corticolous only under exceptional conditions (as in fog forests, or in montane areas, where there is a high incidence of wet days).

‡ I have also found that the southeastern *Calypogeia portoricense* will die when maintained at a relative humidity of 97.5%. This species is typically a mesohygrophyte.

media, *Riccardia latifrons*, *Calypogeia trichomanis* (possibly *C. muelleriana*), *Cladopodiella fluitans*, *Fossumbronia foreolata*, *Mylia anomala*, *Cephalozia bicuspidata*, *Lophocolea heterophylla* (from water-filled ditch), *Lepidozia reptans*, *Riccardia pinguis*, *Pellia epiphylla*, *Cladopodiella fluitans*, *Calypogeia trichomanis*, *Lophocolea heterophylla*, *L. bidentata*, *Lepidozia reptans*, *Lophozia ventricosa*, *Scapania scandica*, *Lophocolea heterophylla*, *Lepidozia reptans*, *Tritomaria exsectiformis*, *Plagiochila asplenoides*, *Lophozia barbata*, *Metzgeria furcata*, *Ptilidium ciliare*, *Lophozia barbata*, *L. bicornata*, *L. hatcheri*, *Lophocolea heterophylla* (corticulous phase), *Radula complanata*, *Frullania dilatata* (near our *F. brittoniae*), *F. tamarisci* (near our *F. asagrayana*), *Ptilidium pulcherrimum*, *Cephaloziella byssacea*, *Porella platyphylla*. It is of interest that some plastic species, such as *Lophocolea heterophylla*, collected at a wide series of sites, showed radical variations in resistance to desiccation. Plant of this species from a water-filled ditch died even if exposed to air with a relative humidity of over 95% for 24 hours; by contrast, the corticolous plants kept at a relative humidity of only 15% for 24 hours showed survival of about 75% of the cells! Similarly, *Lepidozia reptans*, from a peaty site, kept at a RH of 63.5% showed 100% mortality after only about 2 hours, whereas the same species, from a birch trunk, showed 50% survival after 24 hours, when kept at a RH of only 33%. The above data possess a whole series of interesting implications, and corroborate fully the field experiences to which every bryologist is exposed. For example, it is clear from her experiments, that *Lepidozia*, which is very exceptionally epiphytic, survives drought much less well than *Lophocolea heterophylla*.* Similarly the relatively infrequently corticolous populations of *Lophocolea heterophylla*, kept at 15% RH for 24 hours showed 25% of the cells dead, whereas the commonly epiphytic *Ptilidium pulcherrimum*, *Radula complanata* and *Porella platyphylla* showed 100% survival at 15% for 24 hours!

The toleration to desiccation demonstrated in these experiments also shows correlation with the relative humidities measured *in situ*, at some of the points where these species were found. For example, *Calypogeia trichomanis*, with a low toleration for desiccation (all cells dead after 6-12 hours in a relative humidity of 75%) occurred in nature in sites where the relative humidity, at ground level, never dipped below 65-75%. *Lophozia bicornata*, with a high toleration for desiccation (all cells alive after 24 hours at a relative humidity of only 33%) also occurred in nature in sites with a lower humidity (down to 40%). Finally, the extremely drought-resistant *Cephaloziella byssacea* (all cells alive after 24 hours at 15% RH) occurred in areas, in nature, where the relative humidity dipped to 15-25%.

Perhaps the most significant of the experiments reported by Clausen were those that demonstrated that during dry summers, some species show perceptible increase of resistance to desiccation. For example, in *Lophocolea heterophylla*, the same population, collected May 31, showed only isolated survival of individual cells when kept at a humidity of 63.5% for ca. 6 hours, while after a dry summer, on Aug. 31, plants from this population kept at the same humidity, for the same time, showed uniform survival! Similar results, with other species, are reported by Höfler (1945, 1950).

EDAPHIC FACTORS

The Physical Nature of the Substrate.—The structure and consistency of the substrate exerts a great effect on the choice of species that undergo ecesis

* This is again correlated with the extremely rare occurrence of *Lepidozia reptans* at the base of tree-trunks in our region, while on the fog-shrouded higher peaks of the Blue Ridge (at above 5500 ft.), *L. reptans* commonly occurs 3-4 ft. high on bark!

at any one point. A few very simple examples of closely related species suffice here. For instance, the rare *Scapania apiculata* and *glaucocephala* can undergo ecesis only on an organic substrate which is relatively firm, e.g., on moist decaying logs, and with the pH below 5.5; such species as *Scapania cuspiduligera* undergo ecesis only over hard surfaces, such as basic rocks (pH ca. 7.0-7.2). Other species, as the widespread *S. mucronata*, may occur under both types of conditions. In general, the larger the number of substrate-types on which a species may undergo ecesis, the more frequent the species is apt to be.

Often species may occur under apparently widely diverse conditions. For instance, the *Frullania-Radula-Lejeunea* Associale colonizes both the bare bark of trees, as well as bare or nearly bare rock faces. We thus deal with an associale showing a distribution under two very different sets of conditions. However, bare bark and bare rock faces have several characteristics in common, that make the ecesis of members of this associale possible, among them 1) a low level of competition for space, because of the essentially unfavorable environment; 2) a firm surface, on which soil cannot accumulate; 3) extremely intermittent moisture conditions. It is thus evident that very different *appearing* substrates may actually offer much the same environmental conditions to the species undergoing ecesis.

In some cases, the distribution of a species appears superficially almost entirely divorced from the physical structure of the substrate. In that connection, *Preissia quadrata* may be cited as an example. This species is perhaps commonest over rather dry to moist sandstone or limestone rock-walls, especially in southeastern Minnesota. However, it also occurs among sedges and *Scorpidium scorpioides*, *Moerckia hibernica* and *Lophozia schultzii*, in marl bogs (as at Grand Portage). It rarely occurs over the exposed roots of *Thuja* and over *Thuja* logs in marly swamps. It is also found in moist marly ditches, with *Parnassia* (as near Graceton). The species evidently is limited in its distribution by an overwhelming dependency on a high calcium concentration in its substrate, but is extremely tolerant of other environmental conditions. For example, it occurs equally successfully on the dry, insolated sandstone walls in the Whitewater Gorge, Minnesota, and on wet, snow-fed slopes, which are snow-free for less than two months per year, on the northern edge of Ellesmere Island, ca. 500 miles from the North Pole (personal observations made in 1955).

The majority of our species, however, shows a much stricter series of requirements, i.e., exhibits a much lesser degree of toleration. Such species as *Scapania gymnostomophila* (limited locally to the initial and post-initial stages over basic rocks, especially in their crevices), *S. degenerii* (limited to basic rock-pools and near-by moist basic crevices in rocks), *Lophozia schultzii* (limited to marl-tundra and marl bogs), *Cephalozia subdentata* (limited to the exposed, relatively dry surfaces of peat), *Calypogeia suecica* (limited to the initial stages of the decaying-log succession) are more nearly typical. For that reason, the study of the habitat restrictions of the species, and especially of the physical nature of the substrate, is very helpful in acquiring a field knowledge of the Hepaticae.

From the previous examples cited, it should also be clear that it is very

difficult to make any overall generalizations regarding the requirements of the various species as regards the physical nature of the substrate. However, a few generalizations appear sufficiently sound to warrant their citation:

1. Some species apparently never are able to undergo ecesis on substrates rich in organic materials. Our various *Riccia* species (except *R. sullivantii* and *R. fluitans*), fall into this category. These are species usually of inorganic soils.
2. Other species appear never able to undergo ecesis, except on an organic substrate. Such xylolics as *Scapania apiculata*, *Lophozia ascendens* may be cited in this connection. To what degree physical differences in the substrate are responsible here (and in the previous example cited), and to what degree chemical differences are the determining factor in the distribution of these species, is questionable.
3. Some substrates are very rarely effectively colonized because of their unstable nature. For instance, the bark of trees such as *Platanus occidentalis* is almost or quite free of bryophytes, though the bark of *Betula papyrifera*, which exfoliates nearly as freely (but where the exfoliations are more tardily deciduous), may be widely colonized by *Frullania* and *Radula*. Again, loose rocks on talus slopes are usually largely free of bryophytes, since the stability of these is so low that ecesis cannot usually take place. Similarly, sandbars are often quite free of *Riccia* and *Ricciocarpus*, again because rapid shifting prevents any considerable ecesis. It is thus evident that the substrata must have some permanence before it can be colonized, other factors being equal.

Perhaps one of the most important factors governing the ecesis of the varicis species is the ability of the substrate to retain moisture. If the sand barrens of Anoka County are studied, the virtual absence of bryophytes (except for *Polytrichum*) is noteworthy. However, essentially similar sites, where the substrate is of a more compact and water-retaining type (such as loam and clay) are colonized very extensively, especially by *Anthoceros*, *Blasia*, *Pellia* and *Fossumbronia*.

The Chemical Nature of the Substrate.—It is well known that many Hepaticae exhibit very decided "affinities" for specific chemical ions. Whether this is a positive physiological "need" or merely toleration is not always clear; probably in different cases both may be involved. There have been relatively detailed studies only of the relationships of the species to two of these ions, the calcium and copper ions. Undoubtedly, a direct relationship to others exists at times, especially to magnesium (since some species appear very largely restricted to serpentine rocks). On the other hand, a rather large number of species appear strictly restricted to acid rocks rich in silicon. Whether these species occur there because of a physiological "need" for silicon, or merely because they do not tolerate basic substrates is not clear. What is clear is merely that some species appear to exhibit a strict "preference" for siliceous rocks.

Regionally, there are several well-known areas rich in copper, notably the Keweenaw Peninsula of Michigan, and Isle Royale, in Lake Superior (as well as the less known abandoned copper mine on Big Susie I., Minn.). However, at none of these sites have the rare hepaticas *Cephalozia massalongii* and *Gymnocolea acutiloba* (restricted in Europe to copper-rich areas) been found. It would be worthwhile to search these areas carefully for these species.

Since the southeastern corner of Minnesota, as well as most of the immediate area peripheral to Lake Superior, consists of basic rocks, much information has been accumulated regarding the calcium requirements, or tolerances

of some of the species. This is a subject that has been explored in some detail and considerable literature exists on the "calciphile" vs. "calciphobe" nature of the various species.

It is still questionable to what degree pH has any fundamental meaning. Some hepaticologists believe that the actual H ion concentration is the significant factor (for instance, Müller, 1951, p. 157), others believe that very often the hydrogen ion concentration is at best an imperfect reflection of the concentration of calcium ions. This is abundantly clear in the case of some species that appear to be limited strictly to calcareous regions—yet occur in our region under a pH of less than 6.5.* This apparent "need" or "dependency" on the calcium ion has not been established experimentally, but can reasonably be inferred from study of the ecological distribution of such species as *Lophozia grandiretis*, *Preissia quadrata*, *Moerckia hibernica*, *Cololejeunea biddlecomiae*, *Odontoschisma macounii*, etc. *Lophozia grandiretis* occurs either in marl bogs or over peaty soil on basic ledges. In both cases, the pH may be rather low (5.5 or even lower), yet the species occurs only at sites where the underlying substrate is penetrated by considerable calcium ions. If the dependency on calcium did not exist for this species, it should occur elsewhere under conditions of about the same pH, on humus, with no calcareous rock-outcrops or marl nearby. The case of *Preissia* has already been examined in some detail. *Moerckia hibernica* also has a distribution pattern that is inexplicable at first: it occurs over springy slopes, among *Equisetum*; on the sides of wet ditches; in *Thuja* swamps; in wet holes; and in open marl bogs. The most obvious common denominator for all these sites is the fact that a high calcium concentration occurs at each, even though the pH varies very widely. *Cololejeunea biddlecomiae* occurs most commonly over fossiliferous limestone; yet it also occurs over bark, usually of *Thuja*, but only where these trees grow in ravines over basic sandstone or limestone, or when they grow in marl bogs and swamps. For instance, it occurs on the twigs of *Taxus canadensis* in northeastern Iowa, where the latter grows on calcareous sandstones.†

* The attempt to classify species strictly into "calciphile" if occurring above a pH of 7.0, and "calciphobe" if occurring below a pH of 7.0 (as in Meylan, 1924) is wholly artificial and arbitrary.

This is quite clear when a few of the figures given by Scoggan (1950), for the Gaspé, are studied. His tables show that at a pH of 3.8-4.6 the available calcium in bog soil may run from 0.6 to 22.4 ppm, while drip and seepage from cliffs and ledges, showing a pH of 7.2-7.8, thus well above neutral, may show available calcium of only 15.6-29.0 ppm. In other cases, such seepage and drip from calcareous ledges may show a pH only slightly higher (7.8-8.2), but a concentration of available calcium of from 41.2-80.0 ppm. pH measurements, therefore, are not a valid indicator, *per se*, of whether a plant is a calciphile or oxylophyte, even though the calciphiles are rarely found growing under a pH lower than 5.5.

† This example almost parallels that cited by Müller (1938) who found the calciphilous *Metzgeria pubescens*, which usually occurs over basic rocks, on the bark of mountain maple in basic areas. The bark of the latter had an ash with a pH ca. 7.0. These observations by the writer and by Müller show clearly that the distribution of the epiphytes may be clearly correlated with pH conditions, and that (indirectly at least) there may be a definite host-preference on the part of epiphytic Hepaticae. This conclusion is also implicit in the work of Billings and Drew (1938). This was not observed by Brown (1948), who claimed there was no selectivity on the part of the bryophyte. However, the data (table 2) in Brown (1948a) show that the "calciphilous" *Cololejeunea biddlecomiae*

Finally, the case of *Odontoschisma macounii* may be cited. This species occurs occasionally around rock pools (*Scirpus caespitosus* Community), but more often occurs on banks. The pH varies from 7.0 to 5.5, and in a few instances that were measured was somewhat lower. The distribution of this species very clearly is correlated with underlying basic rock-outcrops, i.e., with a high availability of calcium ions.

The pH "requirements" (i.e., tolerances) of many of the species of the area have been studied in detail. These are discussed under the various species concerned in the taxonomic portion of this work. However, the data are graphically gathered together in the following table (table 2), based on over 400 pH measurements that have been made (of over 80 species). The majority of measurements were made from living material, within 12 hours of collection, with a quinhydrone meter, set up and recalibrated at the field station; the measurements of the Frullaniaceae and Marchantiales were made with a Beckmann meter, within 2 days of collection, in the laboratory.*

As is evident from inspection of table 2, some species show an exceedingly wide toleration for variation in pH conditions, and, most often, presumably, variation in concentration of the calcium ions. Among these species are such generally common ones as *Pellia epiphylla*, *Scapania nemorosa*, *Lophocolea heterophylla*, *Lepidozia reptans*, *Cephalozia bicuspidata*, *Blepharostoma trichophyllum*, *Plagiochila asplenoides*, and such weedy species as *Marchantia polymorpha*.

However, the majority of Hepaticae show a much narrower tolerance for variation in pH (and associated conditions). These fall into three categories, which have also been accepted by such workers as Apinis and Diogcs (1935):

1. Species strongly oxylophytic ("calciphobous"), and unable to tolerate pH appreciably above 4.5-4.8. To this group belong such species as:

<i>Mylia anomala</i>	<i>Cladopodiella fluitans</i>
<i>Calypogeia sphagnicola</i>	<i>Gymnocalyx inflata</i>
<i>C. trichomanis</i>	<i>Cephalozia connivens</i>
<i>Odontoschisma denudatum</i>	<i>Bazzania trilobata</i>
<i>Lophozia marchica</i>	<i>Cephaloziella elachista</i>
	<i>C. byssacea</i>

2. Species mildly oxylophytic, and unable to tolerate a pH above 5.0-6.0. To this group belong probably the large majority of our Hepaticae, among them:

<i>Phaeoceros laevis</i>	<i>Frullania eboracensis</i>
<i>Anthoceros macounii</i>	<i>F. bolanderi</i>
<i>Blasia pusilla</i>	<i>Jamesoniella autumnalis</i>
<i>Solenostoma sphaerocarpum</i>	<i>Geocalyx graveolans</i>
<i>Tritomaria exsecta</i>	<i>Nowellia curvifolia</i>

occurs in the marly Bergen Swamp (N.Y.) on 14 species of trees. Away from marl bogs or areas with calcareous ledges, this species is rarely epiphytic in the north, although often so southward.

* The data of Müller (1939) and Apinis and Diogcs (1935) are entered on this table (italics), even though these data cover only a few species.

TABLE 2.—PH data on Minnesota Hepaticae.¹

Species	pH	5.8	5.9	6.0	6.1	6.2	6.3	6.4	6.5	6.6	6.7	6.8	6.9	7.0	7.1	7.2	7.3	7.4	7.5	7.6	7.7	7.8	7.9	
<i>Anastrophylloides hellerianum</i>																								
<i>Anastrophylloides michauxii</i>																								
<i>Anastrophylloides minutum</i>																								
<i>Anastrophylloides sauculus</i>																								
<i>Anthoceros (Phaeoceros) laevis</i>																								
<i>Anthoceros maconii</i>																								
<i>Bazania trilobata</i>																								
<i>Blaesia pusilla</i>																								
<i>Blepharostoma trichophyllum</i>																								
<i>Calypogeia meylensi</i>																								
<i>Calypogeia sphagnicola</i>																								
<i>Calypogeia trichomanis*</i>																								
<i>Cephalozia bicuspidata*</i>																								
<i>Cephalozia connivens</i>																								
<i>Cephalozia media</i>																								
<i>Cephalozia pleniceps</i>																								
<i>Cephalozia byssacea</i>																								
<i>Chirosiopsis pallescens</i>																								
<i>Cleria hyalina</i>																								
<i>Conocephalum conicum</i>																								
<i>Diplophyllum taxifolium</i>																								
<i>Fossombronia foreolata</i>																								
<i>Fossombronia asagrayana</i>																								
<i>Frullania bolanderi</i>																								
<i>Frullania elatior</i>																								
<i>Frullania inflata</i>																								
<i>Frullania riparia</i>																								
<i>Geocalyx graveolans</i>																								
<i>Gymnocolea inflata</i>																								
<i>Gymnocolea famosoniella</i>																								
<i>Gymnocolea autumnalis</i>																								
<i>Leptozia reptans</i>																								
<i>Leptozia heterophylla</i>																								
<i>Leptozia minor</i>																								
<i>Leptozia attenuata</i>																								
<i>Leptozia barbata</i>																								
<i>Leptozia heterophylla</i>																								
<i>Leptozia alpestris</i>																								
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<i>Leptozia alpestris</i>																								
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<i>Leptozia alpestris</i>																								
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<i>Leptozia alpestris</i>																								
<i>Leptozia barbata</i>																								
<i>Leptozia heterophylla</i>																								
<i>Leptozia attenuata</i>																								
<i>Leptozia barbata</i>				</td																				

	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7
<i>Lophozia gillmani</i>
<i>Lophozia ascendens</i> (gracilis)
<i>Lophozia grandiretus</i>	1
<i>Lophozia heterocolpa</i>	2
<i>Lophozia incisa</i>	1	1
<i>Lophozia kunzeana</i>	1
<i>Lophozia muelleri</i>	1	2
<i>Lophozia ventricosa</i>	2
<i>Mannia fragrans</i>	2
<i>Mannia pilosa</i>	1
<i>Mannia rupestris</i> †	2
<i>Mannia sibirica</i>	1
<i>Marchantia polymorpha</i>	2
<i>Myia anomala</i> **	2
<i>Myia taylori</i>	1
<i>Odontoschisma denudatum</i>	2	1
<i>Odontoschisma macounii</i>	1
<i>Pellia epiphylla</i>	1
<i>Pellia nemata</i>	1
<i>Pellia fabroniana</i>	1
<i>Plagiochila asprenoidea</i>	2
<i>Plectocolea hyalina</i>	1
<i>Plectocolea paroica</i>	2
<i>Preissia quadrata</i> †§	1
<i>Ptilidium ciliare</i>	1
<i>Reboulia pulcherrimum</i>	1
<i>Riccardia pinguis</i>	2
<i>Scapania apiculata</i>	1
<i>Scapania cuspiduligera</i>	2
<i>Scapania degeneri</i>	1
<i>Scapania glaucocephala</i>	1
<i>Scapania gymnostomophila</i>	1
<i>Scapania mucronata</i>	2
<i>Scapania nemorosa</i>	1
<i>Scapania saxicola</i>	1
<i>Solenostoma riparium</i>	1
<i>Solenostoma sphaerocarpum</i>	A
<i>Tritomaria exsecta</i>	1
<i>Tritomaria quinquedentata</i>	2

3. Species of circumneutral to distinctly basic substrates (pH 6.0 to 8.0 in all but extreme cases):

<i>Preissa quadrata</i>	<i>Moerckia hibernica</i>
<i>Clevea hyalina</i>	<i>Mannia rupestris</i>
<i>Mannia fragrans</i>	<i>M. sibirica</i>
<i>Lophocolea minor</i>	<i>M. pilosa</i>
<i>Lophozia gillmani</i>	<i>Asterella ludwigii</i>
<i>L. badensis</i>	<i>Scapania cuspiduligera</i>
<i>L. grandiretis</i>	<i>S. gymnostomophila</i>
<i>L. muelleri</i>	<i>S. degenerii</i>
<i>Frullania riparia</i>	<i>Odontoschisma macounii</i>
<i>Cololejeunea biddlecomiae</i>	<i>Pellia fabbrioniana</i>
<i>Tritomania scitula</i>	<i>Cephaloziella arctica</i>
	<i>Reboulia hemisphaerica</i>

Finally, the "nitrophilous" nature of some Hepaticae should be noted. It is readily evident that some Hepaticae and mosses (*Marchantia polymorpha*, *Funaria hygrometrica*, *Leptobryum pyriforme*, etc.) are "nitrophiles." These species appear in great abundance in areas that have been burnt-over or which are manured. H. Hesselman (Medd. fran Statens Skogsforsöksanst. Hfte 13-14, Bd. 2, 1916-1917, pp. ci-cv of English summary) has shown that burning raw humus soil results in a swift and very considerable increase in its nitrifying power; it therefore appears probable that these species are truly nitrophilous, as already indicated by Herzog (1926, p. 69). Richards (in Verdoorn, 1932, p. 382) points out, quite properly, that these species may "like" high concentrations of potassium or of mineral salts generally.* Skutch (1929) and Torrey (1932, 1932a) and others discuss this problem of the invasion of recently burned-over areas by *Marchantia* in some detail.

Although the above species appear to be truly nitrophilous, other Hepaticae have been shown to be able to undergo ecesis on N-free substrates. Griggs (1935, 1937) describes the ecesis of *Cephaloziella byssacea* and

* The suggestion of Richards that *Marchantia* may be not only a nitrophile, but actually shows a "preference" for a high concentration of mineral ions, appears to be borne out by the experimental work of Voth and Hamner (1940), who "found repeatedly in different experiments that plants growing on the various nutrient solutions produced much greater growth than did comparable plants growing on garden soil, even though the plants on such soil were abundantly supplied with water. On some of the nutrient combinations the plants grew and gained more dry weight than did plants observed under field conditions at comparable seasons of the year. The only plants which have been observed growing as rapidly and as large in natural habitats were found in areas from which the vegetation had recently been burned or on the charcoal and ash residues of burned trash piles." This, of course, strongly suggests that the ecesis of *Marchantia* in such bare sites is due to a more positive factor than the lessening of competition by clearing the area; namely, due to consequent increase in mineral concentration.

FOOTNOTE AND KEY TO SYMBOLS USED IN TABLE 2.

¹ It should be recognized, as I have emphasized elsewhere, that in other areas the pH tolerance of certain species may undergo a considerable shift. Also, in the case of those species for which less than 10 measurements are given, it will surely be found that the pH tolerance will show wider variation than here given. In the table, 1 is used to indicate a single measurement; 2 is used to indicate that two, or more, measurements have been made at the identical pH. The measurements of Apinis and Diogucs (as compiled by Müller, 1939) and the additional data given by the latter author are indicated by an A.

The symbols used to indicate several readings at upper and lower extremes (not provided for in Table 2) are as follows:

* A—3.5; ** A—3.0; † 1—8.0; § 1—8.2.

Lophozia bicrenata on N-free volcanic ash. These species, the type members (with *C. rubella*) of the *Cephaloziella-Lophozia bicrenata* Associale (see Schuster, 1949, p. 670), are pioneers in a variety of "inhospitable" sites, and appear to be able to undergo ecesis in exposed, sterile, strongly leached soils where no other Hepaticae occur. This was pointed out by the writer (loc. cit., p. 659-660) who noted the ecesis of this community on strongly leached, sterile acid soils at the edges of exposed ravine-crests.

The absence of certain ions and their effect on growth of *Marchantia polymorpha* has been investigated by Voth (1941), who found that "omission of potassium, calcium, nitrate, or phosphate ions results in characteristic differences in gross appearances of the plants." The lack of potassium produces plants with tan-colored bases and slightly narrower tips. Absence of calcium results in almost immediate death of the growing tips. Deficiency of nitrate and phosphate is indicated by reddening of scales, of rhizoids and of lower epidermis. Plants lacking the former ion become light green, possess few gemmae cups, and fork infrequently; but plants growing on solutions lacking phosphate soon become dark green, have abundant gemmae cups, and because of frequent dichotomy are rosettes. Deficiencies of magnesium and sulphate are not indicated by any characteristic symptoms. These experiments not only prove the extreme dependency of *Marchantia* on nitrogen, but are clearly an indication of the extreme variability that may occur within a species with changes in the edaphic factor-complex. Therefore, it is self-evident that taxonomic conclusions, without experimental data verifying these conclusions, must remain suspect in many cases, in a group of plants showing such a tremendous somatic polymorphism.*

There are scattered other data on the effects of chemical ions and their concentration, dealing largely with *Marchantia*. Lilienstern (1927, et seq.), for instance, found that with a low (0.2%) concentration of nutrient solution in the substrate, *M. polymorpha* was stimulated to produce sexual organs, while a high concentration (0.85%) resulted in suppression of formation of sex organs, but development, instead, of gemmae, or asexual reproductive bodies. However, when the plants were grown in intensive sunlight, they produced sex organs, even if grown in the more concentrated nutrient solution—showing again the complex interdigititation of the environmental factor-

* Fulford, Carroll and Cobbe (1947), using a leafy species, *Leucolejeunea clypeata*, also attempted to show what the effect of specific ion deficiency might be. Though a clear pattern of reaction cannot be deduced from their data, nitrogen deficiency appeared to result in a yellowish to light green coloration, except for the green growing tips. Since the species, unfortunately, has a characteristic pale green color, differences here are slight and difficult to interpret, leading to subjective deductions. Cultures also often showed reversions, but their cause "remains unclear." The authors conclude that "These experiments have added little to our knowledge of the causes of regeneration." The authors also found an increase, often considerable, in cell-size "but since it did not occur in every one of the cultures, and since the amount of increase was variable, it would seem that several environmental factors were probably responsible." Unfortunately, their cultures were grown under several different light intensities (315 ft-c, 150 ft-c, and 80 ft-c direct light) and no indication is often given which cultures, under what light intensities, showed increases in cell-size. Furthermore, with different concentrations of solutions in the closed petri dishes in which the cultures were grown, differences in relative humidity may have existed, which may have modified the cell-size (in addition to differences in light intensity). On careful inspection of their data, it is therefore difficult to conclude whether the effects were due to ion deficiencies, or due to differences in light intensity (and perhaps relative humidity), or due to a combination of these factors. It also seems impossible to deduce very much from such reported data where growth is reported in such wholly vague and subjective terms as "fairly rapid," "rapid," "good," "very slow." If growth had been expressed in numbers of leaves produced per experimental period, and leaf-length, or, better, leaf-area produced, a more objective appraisal of the data would have been possible.

complex, and how difficult it is to generalize from such experiments. The development of sex organs, when the plant is growing on concentrated mineral substrates, if growing in strongly isolated sites, is, of course, well known in nature, where the species often develops luxuriantly after fires. Burning, of course, results in increased concentration of ions, temporarily, and often in increased isolation. Lilenstern also found that, when the concentration of nutrient solution was made even greater (1.75%), the thallus remained small, strongly crispate; the gemmae "cups" remained small and were produced later than when grown in the lesser (0.85%) concentrated nutrient solution. Buch (1920) was able to show a somewhat similar reaction on the part of a leafy hepatic, *Anastrophyllum michauxii*, in which with a low concentration of ions, sexual reproduction was stimulated, while with higher concentration, reproduction by means of gemmae was stimulated.

Müller (1951, p. 156) also cites the case of the ubiquitous *Lophocolea heterophylla*, which is the pioneer species over mineral-rich charcoal and ashes, and states that this is the only species able to tolerate the concentration of chemicals in such charcoal. However, I have made the observation (Manitoulin I., Ontario; Gooseberry R., Minnesota) that several other species come in very shortly after forest fires, on the charred logs and stumps. One, *Cephaloziella rubella*, is notoriously a pioneer species in "difficult" (i.e., "inhospitable") sites; the other species, *Lophozia excisa*, never occurs on decaying logs, but usually on inorganic substrates; it apparently is able to undergo ecesis on charred logs because the immediately underlying substrate becomes essentially inorganic, with a higher concentration of mineral ions, subsequent to charring.

BIOTIC FACTORS

In addition to the climatic and edaphic factor complex, each individual species (and each individual) exists in an additional environment formed by other organisms. These biotic factors that add to the complexity of the environment are perhaps most readily classified into two basic categories a) a set of mutualistic and commensalistic relationships, the consequence of which is either a decided "advantage" accruing to the species, or individual, involved, or at least no perceptible "disadvantage"; b) a set of relationships that, by their very nature, must be inimical to the individual.

MUTUALISTIC AND COMMENSALISTIC RELATIONSHIPS

Evidently mutualistic relationships.—Most terrestrial Hepaticae, especially the humus and wood-colonizing Hepaticae, show a distinct infestation by fungi. Some of these are external, running along the stems or over the leaf-surfaces. Others, however, are internal, infesting the rhizoids and often the cortical, or the lower medullary stem cells (see Pls. 15, 18). In most cases we do not know the effect of the mycorrhizal activity on the nutrition of the host.* It is easily observed, however, that the fungus sometimes results in a profound disintegration of the tissue of the host's stem-medulla

* See, however, Auret (1936), Garjeanne (1903, 1932), Magrou (1925), Racovitzá (1937) and in particular Stahl (1949).

(especially marked in many species of *Lophozia*), and must certainly influence the length of life of the older portions of the plants. In at least two cases there is good evidence that the mycorrhizal fungi are of importance to the hepatic host. Müller (1916, p. 883) has shown that in *Microlepidozia setacea*, a species of acid, nitrogen-poor bogs, the fungus is able to fix atmospheric nitrogen. This occurs, presumably, in a rhizoid-infesting fungus, whose activity results in a nodule-like swelling of the rhizoid-apices. Similarly, swollen rhizoid-apices occur in *Mylia anomala*, *Cephalozia connivens*, etc., and apparently a similar relationship exists there. A second well-substantiated case is that of the subterranean saprophytic hepatic, *Cryptothallus mirabilis*, which is chlorophyll-free. This species (like the gametophytes of *Psilotum*, some *Lycopodium* species, *Ophioglossum*) is dependent on the fungus for its food materials, and therefore exists in a mutualistic relationship with the fungus (which penetrates all of its tissues, including those of the sporophyte).

Commensalistic Relationships.—Under this category are included various relationships whose nature is not clearly understood (mycorrhiza in various Lophoziaceae, in *Marchantia*, blue-green algae in *Anthoceros* and *Blasia*, etc.) as well as relationships that appear to be more casual in nature. Some of these relationships, on more profound study, will prove to be mutualistic—others certainly inimical to the liverwort involved. A few examples follow:

a. Mycorrhiza. Although at times the fungal infection of a liverwort has definite advantages accruing to the hepatic involved, in most cases we do not know what the role of the mycorrhizal fungus is. Such cases as *Lophozia*, where the stem tissue is often largely destroyed on older stems, through mycorrhizal activity, fall in this category. The relationship, as regards certain species of *Lophozia* and *Tritomaria*, appears to be an obligatory one (and we even use the occurrence of modified medullary nutritive tissue, which the fungus inhabits, as a subgeneric criterion); it is almost certainly a relationship of great age and possibly of considerable significance to the hepatic. A somewhat different relationship between fungus and liverwort, equally unclear as regards the effect on the hepatic, is the following:

b. *Anthelia* and surface mycelium. In *A. juratzkana* and other species of the genus, the plants, with drying, almost uniformly become "moldy"—a specific fungus supposedly being associated with the plants. The presence of this supposed surface mycelium which sometimes becomes very abundant on drying plants, is quite inexplicable at present. However, recent microscopic examination has revealed that this "mycelium" is at least partially a web of slender crystals.

c. Myctozoa (Myxomycetes) over leaf and stem-surfaces. Not infrequently a myctozoan occurs consociated with various leafy Hepaticae, the bluish-black, sometimes metallic-appearing sporangia being formed attached to the liverwort.* The relationship is a sporadic one. Kaiser (1913) has noted a similar association with mosses.

d. *Nostoc*, *Anabaena*, and similar blue-green algae, and *Anthoceros* and *Blasia*. The two last-named genera of Hepaticae invariably occur with masses of blue-green algae in the slime-cavities (*Anthoceros*) or in small auricles or domatia (*Blasia*), forming opaque blue-black spots on the thallus. Two independent experiments with *Blasia* show contradictory results: one indicating that the presence of the alga results in better growth of *Blasia*; the other data indicating the opposite. The obligatory nature of the association, in

* Generally involved are, in my experience, species of *Lamproderma (columbium, arcyronema)* and *Physarum flavidum* (determinations by Dr. T. Johnson); according to Dr. Johnson also *Cribaria violacea*.

the case of *Blasia*, is at any rate clear from the fact that the presence of the domatia appears to be a morphological specialization for the "housing" of the alga.*

e. More casual is the relationship between various epiphytic Hepaticae (especially *Frullania* and the Lejeuneaceae), among the plants of which several genera of blue-green algae occur—often in some abundance. Whether the algae derive other than casual shelter is doubtful—while any advantage that may accrue to the liverwort involved remains to be demonstrated.

f. It becomes strikingly evident, even on casual study of the underside of most of the epiphytic Frullaniaceae and Lejeuneaceae, that they have associated with them several apparently distinct species of *Rotifera*, or wheel-animals. These always occur restricted to the lobules, and agree closely with their host in being able to "conduct business" on a very intermittent basis. If a mat of *Frullania* or *Lejeunea* is collected when dry, it is evident that the rotifers are withdrawn into the lobule, and remain dormant. Within a few minutes after the mat is moistened, the rotifers become active, the anterior portion protruding out from the lobule. The interrelationships of the hepatic and the rotifer are a fascinating, but virtually uninvestigated subject, well worthy of future study.

INIMICAL INTERACTIONS TO THE INDIVIDUAL

Food Relationships and Parasitism.—It is well known that Hepaticae are very rarely eaten by small animals. The sole exception, to my knowledge, is *Reboulia hemisphaerica*, the thalli of which are occasionally very much eaten, presumably by some small larvae found with them. A number of species of Hepaticae (*Cephalozia connivens*, *Harpanthus scutatus*, *Lophocolea bidentata*, etc.) are also parasitized by Nematodes (round worms). Generally this parasitism results in the formation of gall-like swellings of the shoot-apices. A number of fungal diseases of Hepaticae have been described, but because of their non-economic nature, are but little known. So far as the writer is aware, no bacterial or viral diseases of liverworts are known.†

Competition.—It seems unnecessary to stress the fact that especially in the lower plant groups (especially the fungi) the extremely high reproductive potential of the species is a characteristic feature of the organism. This has not been equally stressed for the bryophytes in some species of which we find that asexual reproduction (gemmae-formation) may result in the production of over 1,000,000 potential individuals by a square-foot of plants per year (as has been verified by the writer for *Scapania nemorosa*). The very large number of potential individuals produced thus results in a very decided over-abundance of individuals, as related to available space. There is, then, competition between individuals for space, both within the species, and between

* Garjeanne (1930) states that he succeeded "without much difficulty" in cultivating *Blasia* without *Nostoc*. Furthermore, the *Nostoc*-free cultures of *Blasia* could be later "infected" with *Nostoc*. When *Nostoc*-free and *Nostoc*-infected cultures were measured ("Kjeldahl bestimmung") for the amount of nitrogen fixed, "no noteworthy differences" were found. Garjeanne concludes that the nitrogen-fixing activity of *Nostoc* is of "negligible significance" for the *Blasia*. He also found that the domatia were infected with other algae, e.g., *Stichococcus* which "certainly do not assimilate atmospheric nitrogen." Inversely, Molisch (1925) found he could not cultivate *Nostoc*-free *Blasia*, and demonstrated that the *Nostoc* isolated from *Blasia* could fix atmospheric nitrogen. He therefore concluded that *Nostoc*-infected *Blasia* plants had "better" nitrogen "nutrition."

† Nicolas (1932) reviews the scattered literature on both mycorrhizal fungi, and on the various fungi that produce scattered hyphae on the thallus (or leaf) surfaces.

two or more species. In the final analysis, such competition must of necessity be inimical to the individual (though the consequent selection may be advantageous to the species). Therefore, competition is a biotic factor whose exceedingly great significance in conditioning the form of the community cannot be underestimated. The effect of competition between individuals (especially where they develop from the asexual products of a single clonal parent group) is usually expressed in reduced size of the individuals.* The effects of competition between two or more species deserve separate discussion.

SYNECOLOGY

Having briefly examined the individual factors that affect the distribution of Hepaticae, we can now consider the much more complex community relations of bryophytes, and especially Hepaticae. Presuming that the environment is conducive, the disseminules of a plant germinate, grow to maturity and reproduce. This process of adjustment of the plant to a new home, and its growth there ("ecesis") is part of a process by which disseminules of the same or different species come to undergo ecesis together ("aggregation"); between these aggregated individuals that are more or less unequal develops a struggle for space and food ("competition"). As a result of the ecesis of a group of organisms, their environment is usually visibly changed ("reaction"). As an example may be cited the obvious case of the *Nowellia-Jamesoniella* Associale that undergoes ecesis on recently decorticated logs; with the development of this community, the surface of the log undergoes decay; hence there is reaction—a chemical and physical change in the environment. Because of the reaction of the community on the environment (and of competition), there is a gradual change in the community. For example, the corticolous *Nowellia-Jamesoniella* Associale is followed by a more humicolous *Bazzania-Lepidozia* Associale. This change from one community to the next we call "succession."

The competition between individuals and their reaction on the environment result not only in succession but theoretically in a gradual approach to a stable state ("stabilization").† For instance, the humicolous *Bazzania-Lepidozia* Associale may eventually be succeeded, on drier sites, by a *Dicranum-Bazzania* Associale, on moister, more shaded sites, by a *Hylocomium-Bazzania* Associale; these communities are relatively stable, and are not rapidly supplanted by other communities, while the macrovegetation remains in a climax condition.

* This is readily evident at times in such species as *Tritomaria exsectiformis*, which reproduce extensively (and usually almost exclusively) by gemmae, often resulting in dense stands, with the individual plant much reduced in size.

† Stabilization is often a purely hypothetical end that is never quite attained. If we study an *Anastrophyllum michauxii-Diplophyllum taxifolium-Lophozia alpestris* community as existing on a shaded rock-wall, we can see that there is very little succession. The community reacts with the environment and produces a thin humus layer, changing the environment (pH, moisture relationships, especially moisture retention) very considerably; but there is no succession beyond this level because the community has then attained a climax nature. It is virtually stable.

INVASION, ECESIS AND AGGREGATION*

Hepaticae are most generally pioneers; they invade and undergo ecesis in sites that are either bare or have not been covered by higher plants. For that reason, the regions that are best for collecting are generally of extremely diverse nature, for example, 1) the bare bark of trees; 2) rock-faces, and rock-crevices and the crests of cliffs where there is such a thin soil layer that higher plants cannot effectively succeed; 3) recently decorticated logs of trees or stumps, which are still so "raw" that the more humicole mosses and seedlings of higher plants have not been able to undergo ecesis; 4) the continually disturbed alluvial soil among rivers, or the turbulent, spray-washed portions of ravines.

The species of Hepaticae, therefore, by and large, are confined to regions of environmental extremes. This appears to lie partly in the fact that Hepaticae are delicate plants that cannot compete with the larger, more robust and erect-growing mosses (such as carpet the floor of a well-developed Coniferous Climax Forest); they can compete even less with herbaceous and shrubby plants, which often tend to shade them out (while the accumulating dead leaves that are shed each year tend to cover up the mats of bryophytes on the floor of the forest). The Hepaticae therefore are a more or less "temporary" element in the vegetation, except in such areas (as on the faces of cliffs) where higher plants cannot supplant them. This is illustrated most graphically by a study of succession of species on a decaying log, where we may find up to twenty-five species on a recently decorticated log—all more or less pioneer species (such as *Nowellia curvifolia*, *Jamesoniella autumnalis*, *Tetraphis pellucida*, *Cephalozia media*, *C. catenulata*, *C. lacinulata*, *C. macounii*, *Lophozia longidens*, *L. ascendens*, *L. incisa*, *L. porphyroleuca*; *Blepharostoma trichophyllum*, *Lepidozia reptans*, *Geocalyx graveolans*, *Anastrophyllo hellerianum*, *Odontoschisma denudatum*; *Scapania umbrosa*, *S. apiculata*, *S. glaucocephala*, *S. mucronata*; *Tritomaria exsectiformis*, *T. exsectiformis*, *Riccardia latifrons*, *R. palmata*, *Calypogeia suecica*, etc.) (See table 1).† By the time this log, on which we can expect anywhere from 5 to 15 of the above list of 25 species to occur, has disintegrated, all of these species are gone and have been succeeded by mosses and small vascular species (*Coptis*, *Linnaea*, etc.) with persistence at most of such species as *Bazzania trilobata*, one of the few species which appears to be able to persist until the forest-floor climax is attained, even if only as a very minor element.

We therefore deal with a group of plants that is extremely common and often represented by numerous species when we study relatively "raw" and unprepared substrates and sites; these become increasingly fewer (both in species and individuals) as succession proceeds. First they undergo reduction in competition with various mosses, especially the ubiquitous species of

* In spite of the existence of many texts in which these phenomena are treated in more or less general terms, a discussion of them applying chiefly to such small cryptogams is deemed necessary.

† Herzog (1943, p. 268) also has dealt with montane manifestations of this type of community, and finds an equal diversity in the community as is evident from studying the data given here in table 1, and comparing it with the table on p. 268 in Herzog (*loc. cit.*).

Mnium, *Dicranum* and *Hylocomium* and *Thuyidium*; later they are shaded out by vascular plants of various types.

The student of Hepaticae therefore soon learns that his best "collecting grounds" lie in areas where succession cannot readily proceed, because of the slope or nature of the substrate (vertical cliffs) or because of repeated disturbance that inhibits succession (alluvial soil along rivers that is periodically flooded; moist rocks along shores of larger lakes; moist sandy beaches along lake shores), or because conditions are so extreme no other species are able to succeed (dry talus slopes; dry rock-walls; bark of trees). The student of ecology, when dealing with the Hepaticae, therefore deals usually with the initial stages in succession: a microsuccession of which very little is known. In the following section on communities the writer occasionally calls attention to the more obvious successional tendencies; in many cases succession, however, is something one can impinge but not prove.

We know very little regarding the concrete factors that govern the invasion of particular sites by particular species. In many cases chance appears to be the dominant factor. As a critical example, the writer may mention his experience with the *Scapania degenerii*-*Odontoschisma macounii* Associate of basic, sunny rock-pool margins. It appears to be purely a matter of chance whether we have *Scapania degenerii* as the initial species here undergoing ecesis on the bases of *Scirpus cespitosus* hummocks, or whether *Scapania irrigua* undergoes ecesis here. The two species of *Scapania*, under the given conditions, appear to be nearly equivalent ecologically. Under some conditions *S. degenerii* occurs (Long I., Temperance R., Big Susie I., etc.); under other conditions *S. irrigua* occurs (Grand Marais, Sailboat I.); not infrequently the associate consists of mixed *S. irrigua* and *S. degenerii* (as on Sailboat I., and at Grand Marais).

Similarly, on rather dry, shaded rock-walls the invasion of one species or another and resulting composition of the "patches" or "consocies" that are formed, are extremely haphazard. *Anastrophyllum minutum* may undergo ecesis first, or *Tritomaria quinqueidentata*, or *Lophozia alpestris*, or *Diplophyllum taxifolium*, or *Andreaea rupestris*; we therefore can get "patches" formed purely by these species individually, or various facies formed by any combination of 2 or 3 or 4 of these species. Adding to the complexity, other minor species may crop up and become frequent in this society, such as *Lepidozia reptans* and *Lophozia barbata*, occasionally *L. hatcheri*. These species occasionally are common enough so as to appreciably change the appearance of the society.

Again, the pioneer species on the bark of a tree may consist of *Radula complanata*, *Frullania eboracensis*, *F. bolanderi*, *F. oakesiana*, *F. selwyniana*, together with a larger number of pioneer mosses. It appears to be entirely a haphazard matter which species invades first, and the consequent nature of the society therefore is a pure matter of chance. It may consist of only one, or any two or three or four of these species. For instance, in studying the *Frullania*-*Radula*-*Porella* Associate on the bark of *Thuja* in the foggy forest along Lake Superior north of the Cascade R. in Cook Co., the writer found an enormous degree of variations. Ignoring the mosses and lichens (which

superimpose even a greater pattern of variation), we find the following combination of species:

1. *Frullania bolanderi*
2. *F. bolanderi* + *F. eboracensis*
3. *F. eboracensis* + *F. oakesiana*
4. *F. oakesiana* + *F. bolanderi*
5. *F. bolanderi* + *Radula complanata*
6. *F. eboracensis* + *R. complanata*
7. *F. eboracensis* + *R. complanata* + *F. oakesiana*

If we include variation under identical conditions on *Thuja* that obtains at the Encampment River, we get in addition:

8. *Frullania oakesiana* + *Lejeunea cavifolia*
9. *F. eboracensis* + *L. cavifolia*
10. *F. eboracensis* + *L. cavifolia* + *Radula complanata*
11. *F. eboracensis* + *L. cavifolia* + *R. complanata* + *Porella platyphyloidea*

The largest factor that appeared to govern the nature of the bryophytic associule was chance (combined with time). The pure matter of chance as to which species underwent ecesis first (or which two species or three species), together with the time intervals that elapsed between ecesis of other species subsequently would result in extremely different appearing communities or "patches". This, of course, is the case only if the species are ecologically nearly equivalent (as appears to be the case under the above conditions, on slightly moist bark under shaded and usually rather humid conditions).

If we take a relatively complex phenomenon, such as the composition of the pioneer society obtaining on recently decorticated logs (on which the superficial layer of xylem has undergone negligible disintegration) we find even more variation. Ecesis by any of the 25 pioneer or near-pioneer species may occur, such as *Jamesoniella*, *Lophozia ascendens*, *Calypogeia suecica*, etc. An analysis of the large number of combinations of species with a variable number of species consociated leads to the conclusion that there is an infinite amount of variation possible in the nature of the associule, because of the two factors of chance and time (ignoring all of the additional complexity imposed by the undoubtedly existence of internal competition and internal microsuccession within the associule). This is clear from table 1, which deals with only the hepatic element represented.*

In such clear-cut cases when we have invasion possible by a discrete number of ecologically nearly equivalent species, one tends to lean decidedly towards Gleason's Individualistic Concept of Plant Association (see Gleason, 1939). One also is almost forced to consider the environment as the governing feature of plant invasion. Environment plus chance plus time govern what species (out of a larger number of "candidates") shall undergo ecesis. Hence, the species-rich and polytypic bryophyte communities (and especially

* The study, by Herzog (1943) of eleven decaying logs in the montane forest of the Black Forest of Germany reveals a strikingly similar degree of variability. Herzog's study was based on a *Tetraphis pellucida* Facies of the community, in which *Nowellia* and *Jamesoniella* were absent or infrequent.

pioneer communities or communities where there has been very little succession) are *much more easily defined* on the basis of the environment than on the basis of the composition (coverage, fidelity, etc.). One reaches the inevitable conclusion that the composition of the society is a matter of little moment, since it is the result of the interoperation of so much inherent chance that the practice of naming societies *after* the more "constant" of the plants composing it has little to recommend it.* Herzog (1943) has advanced an identical opinion.

The extreme variability of many of the initial stages therefore is due in part to the fact that very frequently a larger number of ecologically nearly equivalent species may undergo ecesis on the same site. A further factor tending to lead to such heterogeneity of the community results from the gregariousness or sociability of many species of Hepaticae (and mosses). This leads to large patches consisting exclusively of one (or two) species, sometimes feet or yards across, existing side by side with patches of different but ecologically similar species (existing and having undergone ecesis under identical conditions). This extreme heterogeneity of these pioneer and near-pioneer societies leading to an extraordinarily mosaic nature of the vegetation is due in large part to the tendency towards a high level of constant reproduction by means of asexual reproductive structures (gemmae, caducous leaves). Hence, if a species has a slight advantage in time (i.e., undergoes ecesis earlier) it tends to form large, pure patches, due to the extraordinarily high reproductive potential.†

The extraordinary variability of the unistratal bryophyte (and bryophyte-lichen) communities, especially of the pioneer or near-pioneer communities existing under conditions where there is little succession, is one of the most notable features of vegetation. As we have seen, this is due to a combination of factors: chance + time + extremely high reproductive potential via vegetative reproduction and spores + a near ecological equivalence of often a large number of species under a given set of conditions.

In spite of this overwhelming variability, we find that there are decided patterns that govern invasion and succession. If we do not allow ourselves to be overwhelmed by the complexity of variation, we will see that, within certain limits, the pattern of invasion and succession follows rules, however flexible these may be. Hence, on any particular site, at a specific point in invasion and succession, we tend to have recurrence of the same species (or, at least, of one or more of a group of nearly equivalent species). In a following section an attempt is made to distinguish between some of these resulting unistratal communities.

* It is only subsequent to succession towards the climax that there is general reduction to a relatively small number of species; it is only then that the concepts of fidelity and constancy develop a degree of usefulness.

† I have estimated that a patch of *Lophozia grandiretis* a square centimeter across will produce in excess of 10,000 gemmae per growing season. Similarly, judging from an examination of individual gemmae-masses on plants, a square foot mat of *Scapania nemorosa* will produce in excess of a million gemmae per year under favorable conditions. The tremendous ability of these asexually-reproducing species to almost suddenly carpet recently bared areas is thus a striking feature of the species, leading to the formation of closed, pure patches analogous to the consociations we get in the climax forests.

SUCCESSION

As with the higher plants, aggregations of bryophytes are generally not static units, but are in an active or dynamic relationship to each other, since there is competition by the individuals (of one species, and of the different species).* In addition, the initial species of a community *react* on their microenvironment, resulting in the production at times of physical conditions that are no longer favorable for their growth.†

From this, it is evident that any single type of habitat supports in general several communities. This is well-known and is stated as follows by Richards (1938):

The explanation for this fact appears to be that the different associates in the same habitat stand in a successional relationship to each other. Thus, these associates, like communities of higher plants, are not static, but undergo development. . . . Successions like these within the control of a major community such as wood, have been termed serules (Clements, 1936).

It should be noted, however, as has been stressed in the previous section on Invasion, that many of the pioneer communities of bryophytes (and lichens) undergo extremely little or no succession. They tend to form more or less closed societies, often formed by a mosaic of heterogeneous patches of ecologically nearly equivalent species (or a combination of two or more such species). These patches under some conditions are very permanent, and undergo very slow or almost no succession when occurring on sites such as the dry vertical faces of rocks, or on wet rocks around waterfalls.

For instance, on a rather exposed, dry rock-face we may get the invasion of lichens, such as *Umbilicaria dilenii*, *Gyrophora*, etc.; these lichens grow extremely slowly, because of the extraordinarily inhospitable environment. Eventually, Hepaticae of one or two species (*Frullania asagrayana* and occasionally *Radula complanata*) may undergo ecesis on these lichen-covered surfaces, and competition between the Hepaticae and the lichen is initiated. In this competition the Hepaticae often appear to be favored because of a somewhat more rapid rate of growth: hence they tend to grow over and shade out

* This is most readily evident when we examine the earliest stages of succession on such habitats that very obviously show rapid succession, such as decaying logs. The first species that invade are such decumbent or appressed types as *Jamesoniella autumnalis*, *Nowellia curvifolia*, *Lophocolea heterophylla*, *Cephalozia catenulata*, *C. media*, *Riccardia latifrons*, etc. Later stages, evidently later successional because the logs are now strongly disintegrated, show that these species have been nearly or quite eliminated because of succession by a group of erect or caespitose species in most cases (*Dicranum* spp., *Tritomaria exsectiformis* in some cases, *Anastrophyllum michauxii*, *Bazzania trilobata*, *Tetraphis pellucida*, etc.). Obviously the more delicate and more decumbent initial species are unable to compete on favorable terms with the larger and more erect later species, which are easily able to crowd them out.

† A very obvious example is the deposition of a humus layer by the gradual growth of calciphilous types, such as *Odontoschisma macounii*, on ledges. This peaty layer, formed of dead and decaying older portions of the plants, effectively reduces the pH of the substrate and gradually brings the plants out of contact with the calcium-rich rock-surfaces, resulting in the gradual development of an environment very different from that under which the *O. macounii* underwent ecesis. Gradually, the physical conditions become such that other species (*Blepharostoma trichophyllum*, *Lepidozia reptans*, *Lophozia grandiretis*), more strongly humicolous, are able to replace the *O. macounii*.

the lichens (but the inverse also happens to a minor degree). Such succession has been studied in detail on the Susie Islands (Big Susie I., Belle Rose I.), and appears to be an extremely slow process. Finally, after a rather thick lichen-*Frullania-Radula* layer accumulates, there may be a minor amount of invasion by xeromorphic ferns (such as *Dryopteris fragrans*), especially if crevices are present in the rock. A climax community, or associule, thus results that is dominated by lichens, or jointly dominated by lichens and *Frullania* and *Radula*, with *Dryopteris fragrans* (more rarely *Cystopteris fragilis* or *Polypodium vulgare*) as occasional species that one might almost consider as "postclimax" in nature.

Without attempting to treat any community in detail, it may be instructive to examine a few examples of succession (and sometimes lack of succession) to illustrate the points raised above.

1. The *Scapania-Lophozia* Associule. The various polymorphic faciations of this ancient, widespread holarctic associule are dealt with in the succeeding section on communities. Often it is difficult to prove successional patterns here, but a few are obvious.

On bare rocks (bare, often even of lichens) we may get an initial stage formed by *Anastrophyllum michauxii*, often forming large mats. This may form (a) a closed society (as on Big Susie I.), when the plants occupy relatively xeric, sunny sites, and where succession by more mesic species is virtually impossible; in such a case, we have an evidently climax *Anastrophyllum michauxii* Consociule. (b) An open society (as on shaded, moist ledges, on the southern end of Lucille I.) where the species may be pioneer in large mats, in other places undergoing ecesis at about the same time as several other species. Here we find succession from the *A. michauxii* pioneer stage to a mixed stage formed by *A. michauxii*, *A. minutum*, *Lophozia ventricosa* (or *silvicola*) and a few mosses. This in turn is succeeded, subsequent to humus formation, by an even more complex community, including the above species, plus *Lepidozia reptans*, *Blepharostoma trichophyllum*, etc. Finally, this is succeeded upon deposition of even more humus (resulting in a thick, peaty, water-retaining layer, i.e., more constantly moist and hygric conditions) by a *Sphagnum-Lepidozia reptans-Blepharostoma trichophyllum-Cephalozia media-Lophozia ventricosa* (*silvicola*) community. The latter forms swelling, wet, thick tufts and is, at that point, climax in nature, or, perhaps more nearly "disclimax" in nature, since its weight is so great that freezing during the winter prevents succession to a further point (due to periodic breaking loose of the moss-mats; then a return to the bare rock-face, which may again be invaded by the *A. michauxii* pioneer community). Careful study of this second type of community has demonstrated all stages of this process, including the denudation cited, and the following return to the pioneer *A. michauxii* stage. Obviously, under even slightly different conditions of pH, moisture, and light, a somewhat (or even greatly) different successional picture will obtain.

2. On wet rocks at the very edge of Lake Superior, in the actual wash of the waves, on shaded rocks, we find *Marsupella emarginata* forming a pioneer community. Under extreme conditions (i.e., where actually submerged for

part of the time) this forms a closed associate here with no further succession. However, when growing at a slightly higher level (in the shaded spray-zone) we find the *Marsupella* coming in as a pioneer, but soon its mats serve as a matrix for the ecesis of *Scapania subalpina* and *S. undulata*. Depending on the most minute microenvironmental conditions, a closed community of *Marsupella* + *Scapania subalpina* + *S. undulata* results, or the *Marsupella* is eliminated by competition, resulting in a *Scapania subalpina* + *S. undulata* community, beyond which we find no succession, under the given conditions. (This community was studied at Little Susie I.)

3. Under conditions that are only slightly different (as on the vertical rock-walls on Porcupine and Belle Rose Isls.), the wash and spray zone supports a pure consociate of *Scapania undulata*, without the slightest admixture, showing not the slightest evidence of succession.

4. In strongly shaded cuts through these vertical ledges, away from the spray-zone, but in an area where the adjacent wave-action and water level conspire with constant shade to result in a microenvironment with a constantly very low saturation deficit, we find a *Diplophyllum taxifolium* var. *macrosticta* community.* This is typically quite pure, under extreme shade conditions (light less than 1/80), and then forms a closed community, forming paper-thin, easily loosened mats (as on Big Susie I.). However, if the light intensity is slightly greater (1/60 or more) we find *Blepharostoma trichophyllum* and *Lepidozia reptans*, occasionally *Lophozia alpestris* and *L. silvicola*, succeeding the *Diplophyllum taxifolium*. Again, we see that the ability of the initial community to persist depends on the extreme physical conditions of the initial stages, i.e., it leads to the conclusion that the pioneer species are often those which have such a low competition-coefficient that they can persist only where other species cannot undergo ecesis.

The above examples are chiefly of communities which show little or no succession; i.e., we deal with communities which become "closed" (to ecesis by other species) either soon after invasion by the pioneer species, or after one or two successional stages have been passed. In other cases, we deal with much more "open" successions, where a site not only can be invaded by a wide variety of species (leading to the most diverse initial stages), but where there is a diversity of possible successional stages, formed by a rather great diversity of species. Perhaps the most polymorphic of such "open" successions are the various stages of the *Nowellia-Jamesoniella* Associate of decaying logs, and the *Lophozia-Scapania* Associate of moist rocks. These serve as examples to illustrate "open" successions, which are of so infinitely more complex a nature that delineating them in detail is impossible with our present understanding.

THE CONCEPT OF THE STRATAL COMMUNITY

Vegetation (except in parts of the Arctic Tundra Zone) consists of a number of strata, or layers: a layer of tree-like plants, under which we find a layer of shrub-like plants, under which in turn is a layer of herbaceous plants.

* An entirely similar community results on the shaded underside of erratic boulders, lying adjacent to Caribou Spring (where ice-cold water runs all summer long, and where snow persists for a long time) on Mt. Katahdin, Maine, in the Alpine Tundra.

Under the latter, finally, is a layer that includes the so-called "muscoid" plants, of Warming, which includes, in addition to Hepaticae, mosses and lichens, various small animals and often blue-green algae, etc.

The concept of vegetation as a group of strata is one that has undergone a gradual development, and has been best developed by the Scandinavian botanists. It has also been found that any one layer society formed by mosses, Hepaticae and lichens, does not occur restricted, of necessity, to one vegetation type. For instance, we have a *Mylia taylori* Community or Associate, which recurs over rock-faces in montane areas, both in the Tundra, as well as in the Coniferous Forest. Again, an epipetric community formed by *Cephalozia bicuspidata*, *Lophozia apertis*, *Gymnocolea inflata* and *Scapania* species (*nemorosa*, *curta*) etc., occurs above tree-line in the Tundra, is frequent in the boreal Coniferous Forests, on rock-outcrops, and occurs rarely even in the Deciduous Forests (as in central and western New York; see Schuster, 1949). The recurrence of the various cryptogamic associates under various forest types is one of the most characteristic features of these unistratal communities. This has led to the development of the concept of "twin-formations" of "homologous series" or "combination cycles." For that reason, the development of the study of moss societies has had to be largely independent of the study of the forest types. Since bryophytes are never dominant species in the composite associations as a whole, but merely constitute a small part (except in the Tundra), bryocoenology cannot deal with the associations, or units, as a whole.*

Hepaticae (and mosses), because of the relatively narrow limits within which they vary in size, are generally regarded as belonging to a single "stratum."† The stratum to which Hepaticae belong includes, obviously, a large variety of other plants (and animals), such as lichens, mosses, various algae (especially blue-green algae), diatoms, and bacteria as well as fungi and myctozoa. An integrated treatment of all of these elements present in such a stratal community is impossible here, because of limitations of knowledge and space. For instance, Heinis (1937) found that on studying alpine plant polsters quantitatively, he found complex biocoenoses with *Sphagnum* polsters, consisting of food chains embracing holophytes, herbivores,

* It must also be recognized that, since the bryophytes (and lichens) are restricted to microenvironments, a single forest type will support a large number of bryophyte-lichen communities. Richards (1938) has stated this well: "Anyone who has closely examined the bryophyte vegetation of a wood will realize that the bryophytes in it grow under a great variety of conditions. A species on the branch of a tree, for example, is living under quite different conditions from one growing on the ground. A wood offers, in fact, a number of distinct habitats for bryophytes which differ not only in substratum (which may be soil, humus, bark or sometimes rock), but also in respect to illumination and atmospheric humidity, i.e., in the microclimate. As a result of this variety of habitats, where the general climate is favorable, a wood will contain a number of bryophyte communities, each with a distinctive floristic composition. Often these communities are so different that some of them have no species in common. . . ."

† This is not strictly correct, since there is microstratification even within this layer. For instance, a decaying stump occupied by a dense cover of *Tetraphis pellucida*, a frequent moss in our region, at the base of which occur isolated, spreading, horizontal stems of *Cephalozia media*, a common humicolous hepatic, illustrates a "unistratal" society with distinct stratification within it.

carnivores, dominated by plants such as bacteria, diatoms, and protozoa and nematodes; in the detritus of these hummocks of *Sphagnum* he found 56 species of microorganisms, including Diatomaceae, flagellates of various kinds, Protozoa (Ciliata and Rhizopoda), Rotaria and Nematoda.

Even such a superficially simple "unistratal community" as the *Frullania eboracensis* consociation of the *Frullania-Radula-Porella* Associale represents a complex biocoenosis. Study of a patch of plants some 8 centimeters square by the author showed the presence of several kinds of blue-green algae, of *Chroococcus*, over five kinds of diatoms, various small protozoans, as well as of a species of rotifer confined to the "lobules" of the *Frullania*. In addition, among the *Frullania* plants occurred isolated individuals of a plant bug (*Corythuca*, a Tingid) apparently undergoing hibernation. Critical study of such a corticolous associale would show, probably, a combination of up to 30-40 species of plants together with probably many small animals, running from Protozoa and Rotifera up to Nematoda and Arthropoda. Such stratal communities are variously called unions (Lippmaa) synusiae, lamiations (Clements), or merely layer societies or "stratal societies." More recently Richards (1938) has used the Clementsian term "associale" for essentially this same concept—in part for mere portions of what are frequently called unions. The writer (1949) followed Richards in using the term associale for the unistratal societies constituted largely of Hepaticae and mosses. This usage (or the use of the non-committal term "community") seems preferable to the use of the better established terms "union" or "synusia," since these cryptogamic communities are still not sufficiently rigidly delimited, and since many of the communities we call "associales" may represent stages in development (i.e., "lamiae" or portions of a "serule") or localized facies (of a larger-conceived "union").*

The use of the term "union" or "associale" does not necessarily imply succession. The classical diagrams or schemes in which succession from a bare vertical rock-wall to a dense climax forest is implied are unduly naive for the modern worker to follow. The field student, after many seasons of observation, will often see that these unistratal bryophytic (or bryophytichen) communities are of great permanence, and fulfill many of the requirements of climax societies. Since in most cases succession cannot be proved (and often not even the direction of succession), without much more critical work than has been done locally, the terms "union" and "associale" are used here essentially in a descriptive sense, without any effort, except where too obvious to oversee, to point out successional tendencies.†

* It must also be emphasized that the tremendously complex problem of the unistratal, cryptogamic communities of the boreal and deciduous forest regions of eastern North America has barely been touched. The present account is merely a simplified beginning, based on six years of field work. A definitive account would entail many decades of study, including not only the Hepaticae involved, but also the mosses and lichens. In general the latter two groups are more common, and communities dominated by Hepaticae are, in general, quite infrequent. As a consequence, the present account deals with only a minority of the cryptogamic communities present in the area. For this reason, and because of the doubtful status of many of the cryptogamic communities, the term "associale" or "community" is preferable.

† Insofar as obvious succession can be demonstrated, this is briefly dealt with in the preceding section on Succession.

(To be concluded in 57(2).

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